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Salmonella spp. in low water activity food: Occurrence, survival mechanisms, and thermoresistance

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Abstract

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The occurrence of disease outbreaks involving low-water-activity (a_w) foods has gained increased prominence due in part to the fact that reducing free water in these foods is normally a measure that controls the growth and multiplication of pathogenic microorganisms. *Salmonella*, one of the main bacteria involved in these outbreaks, represents a major public health problem worldwide and in Brazil, which highlights the importance of good manufacturing and handling practices for food quality. The virulence of this pathogen, associated with its high ability to persist in the environment, makes *Salmonella* one of the main challenges for the food industry. The objectives of this article are to present the general characteristics, virulence, thermoresistance, control, and relevance of *Salmonella* in foodborne diseases, and describe the so-called low-water-activity foods and the salmonellosis outbreaks involving them.

KEYWORDS

contamination, food poisoning, microbial survival, moisture, public health

1 | INTRODUCTION

Salmonella is considered one of the main pathogenic bacteria responsible for foodborne illnesses worldwide (Priya et al., 2020). Its transmission can occur through food and water contamination, and contact with contaminated animals and humans (Christidis et al., 2020; Ferrari et al., 2019).

The genetic variability of this pathogen favors its survival and dissemination in a wide variety of environments, hosts, and its immune system (Tanner & Kingsley, 2018). The presence of this bacteria can be even more worrying depending on the composition of the food and also on the susceptibility of the host (Crucello et al., 2019). Epidemiological studies show that the infecting dose can range from 10^5 to 10^8 cells, and $\leq 10^3$ in immunocompromised people (Ministry of Health [Brazil], 2011).

Considering *Salmonella* pathogenicity, its ability to survive, and to cause illness, the objectives of this review are to present the general characteristics, virulence, thermoresistance, control, and relevance of *Salmonella* in foodborne diseases, and describe the so-called low-wateractivity foods and the salmonellosis outbreaks involving them.

2 | PRINCIPAL TEXT

2.1 | General features

The genus Salmonella is divided into two main species: Salmonella enterica and Salmonella bongori. Salmonella enterica also has six subspecies: enterica, arizonae, salamae, diarizonae, indica, and houtenae. Salmonella enterica



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subspecies *enterica* represents 99% of cases of foodborne disease outbreaks (Lamas et al., 2018). In addition, more than 2600 different serovars have been reported (Yang et al., 2019).

Salmonella belongs to the Enterobacteriaceae family. They are Gram-negative, rod-shaped, mobile, facultative anaerobes, and nonsporulated bacilli. For growth, the optimum temperature ranges from 32 to 35°C, with a pH in the range of 4–9, with 6.5–7.5 being the ideal (Jajere, 2019).

2.2 | Virulence factors and pathogenicity mechanisms

Salmonella virulence is multifactorial and complex, involving structures (fimbriae, flagella, effector proteins) and its capacity for invasion, multiplication, and evasion of the host immune system (Fardsanei et al., 2018).

Most virulence-related genes in *Salmonella* are found in *Salmonella* Pathogenicity Islands (SPIs). SPIs cover large regions of the chromosome that encode several virulence factors (Dos Santos et al., 2021) and, so far, 17 SPIs have been described (Fowoyo, 2020).

SPI-1 and SPI-2 are the most studied and both encode the Type III Secretion System (T3SS) that forms a channel in the host cell membrane, allowing bacterial effector proteins to be secreted inside these cells. These proteins induce modifications in the actin cytoskeleton, allowing the internalization and proliferation of the pathogen (Espinoza et al., 2017; Nieto et al., 2016).

SPI-1 is initially characterized as an invasion island. It is present in all *Salmonella* species and subspecies and has the necessary genes involved in nonphagocytic cell invasion, the T3SS secretion, activation of innate immune pathways (Lou et al., 2019), and the gene cluster responsible for iron capture (Sever & Akan, 2019).

SPI-2 is related to the ability of this bacterium to survive in phagocytic cells and to replicate within SCV (*Salmonella* Containing Vacuole) in eukaryotic cells (Liew et al., 2019).

The others SPIs are mainly involved in macrophage survival; replication; production of proteins, adhesins, and toxins; and fimbriae encoding (Ilyas et al., 2017; Klingl et al., 2021; Singh et al., 2018).

In their original habitats, most bacteria are found in aggregated communities composing a biofilm, responsible for microbial protection, propagation, and permanence in the environment and capable of increasing their resistance against antimicrobials and sanitizers. These biofilms are composed of polysaccharides and proteins, called exopolysaccharides (EPS), and changes in these components can interfere with the virulence potential of the associated pathogens (Zhao et al., 2017). Biofilms extracellular matrix have a major function in the survival of *Salmonella* under unfavorable environmental conditions (Merino et al., 2017; Wang et al., 2013). Fimbriae play an important role in the adhesion of *Salmonella* spp. to the target cell (Xu et al., 2021), and cellulose provides biological, mechanical, and chemical protection against the environment (Čabarkapa et al., 2019).

2.3 | Importance of *Salmonella* in foodborne diseases

Worldwide, foodborne diseases represent a major public health challenge. In the United States, each year, approximately 1.2 million cases of foodborne diseases are mostly caused by *Salmonella* Enteritidis, *S*. Typhimurium, and *S*. Newport (CDC, 2016; Tack et al., 2019). The European Food Safety Authority (EFSA, 2019a) showed that *Salmonella* was responsible for 11,581 (30.7%) human outbreaks during 2018, a higher number compared with 2017 (20.6%).

According to Ministry of Health (Brazil) (2019), between 2009 and 2018 *Salmonella* spp. was the second leading cause of foodborne diseases in the country, representing 11.2% of reported outbreaks. Updated data from the Epidemiological Bulletin of the Health Surveillance Secretariat (Ministry of Health [Brazil], 2020) showed that between January 2016 and December 2019, the prevalence of *Salmonella* spp. outbreaks increased 14.9%. Voss-Rech et al (2019) and Mendonça et al. (2020) indicated *S*. Typhimurium, *S*. Enteritidis, *S*. Infantis, *S*. Heidelberg, *S*. Newport, *S*. Hadar, *S*. Mbandaka, and *S*. Senftenberg as the most common serovars in Brazil.

Meat, eggs, and milk are not the only ones that can be contaminated by *Salmonella*. The number of salmonellosis associated with low-water-activity foods is gaining prominence. Many of these foods do not undergo cooking processes, can be readily consumed, and have a prolonged shelf life at room temperature (Carrasco et al., 2012; Farakos et al., 2013). Another important factor is that water activity (a_w) reduction is a control strategy adopted by the industries themselves precisely to prevent the proliferation of pathogenic microorganisms in food (Ashenafi, 2012).

Initially, powdered milk, nuts, chocolates, dried fruits, and flours were considered safe foods because of their suppressed microbial growth, either because of their low a_w value or because they undergo crystallization, dehydration, desiccation, and lipid oxidation, which are not favorable for microorganisms. However, many pathogens are surviving in these conditions for months or even years (Table 1), which represents a reason of great concern for industries (Enache et al., 2017; Garces-Vega et al., 2019).

TABLE 1 Salmonella survival in low-water-activity ingredients and foods

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| Serotypes | Foods | $a_{ m w}$ | Survival time | Reference |
|--|--|--------------|---------------------------------------|----------------------------------|
| S. Eastbourne | Milk chocolate | 0.41 0.38 | >9 months at 20°C 9 months at 20°C | Tamminga et al., 1976 |
| S. Eastbourne | Bitter chocolate | 0.51 0.44 | 9 months at 20°C 76 days at 20°C | Tamminga et al., 1976 |
| S. Infantis and S. Tennessee | Pasta | | 360 days | Rayman et al., 1979 |
| S. Saintpaul, S. Rubislaw, and S. Javiana | Paprika powder | | >8 months | Lehmacher et al., 1995 |
| S. Enteritidis | Halva | 0.18 | >8 months under refrigeration | Kotzekidou, 1998 |
| <i>S</i> . Typhimurium DT104 | Egg powder | 0.2–0.3 | 8 weeks at 13 or 37°C | Jung & Beachat, 1998 |
| S. Agona, S. Enteritidis, S. Michigan, S. Montevideo, and S. Typhimurium | Peanut butter products | 0.2-0.3 | 24 weeks at 5 or 21°C | Burnett et al., 2000 |
| S. Enteritidis PT 30 | Almond kernels | | 550 days at 20.4 and 23°C | Uesugi et al., 2006 |
| S. Napoli, S. Enteritidis, S. Oranienburg, S. Montevideo, S. Poona, S. Typhimurium LT2, and S. Senftenberg | Cocoa butter oil/crushed cocoa husks/crushed hazelnut husks | 0.2 | 21 days at 5 or 21°C | Komitopoulou & Peñaloza, 2009 |
| S. Anatum, S. Enteritidis PT 9c, S. Enteritidis PT 30, S. Montevideo, S. Oranienburg, and S. Tennessee | Almond kernels | 0.4 | 12 months at 19.4 and 24°C | Kimber et al., 2012 |
| S. Typhimurium | Peanut butter fondant | 0.65-0.69 | 1 year | Nummer et al., 2012 |
| S. Anatum, S. Enteritidis PT 9c, S. Enteritidis PT 30, S. Oranienburg, and S. Tennessee | Raw nut | 0.4 | 12 months at 20.4 and 23°C | Blessington et al., 2012 |
| S. Tennessee and S. Typhimurium DTI04 | Peanut butter | 0.3-0.6 | 12 months at 20°C | Kataoka et al., 2014 |
| S. Anatum, S. Enteritidis PT 9c, S. Enteritidis PT 30, S. Oranienburg, and S. Tennessee | Raw pecan grains | | 12 months at 24.4 and 22°C | Brar et al., 2015 |
| <i>S</i> . Senftenberg 775W, <i>S</i> . Newport, <i>S</i> . Typhimurium, and <i>S</i> . Tennessee | Wheat flour | 0.46-0.45 | 1 year at 20°C | Michael et al., 2022 |

2.4 | Salmonella outbreaks in foods with low water activity

The water that is not chemically linked to other substances is called free water, and it represents a favorable medium for the growth of bacteria, yeasts, and molds. This free water is measured by the activity of water (a_w), defined as the ratio between the vapor pressure of a solution and the vapor pressure of pure water at the same temperature. The a_w ranges from 0 to 1, where 1 represents pure water, where microbial growth is not possible. Thus, the addition of nutrients gradually reduces the a_w value of foods (Barbosa-Cánovas et al., 2020; Tapia et al., 2020). According to Jin et al. (2018), to consider food as having low a_w , it must have values lower than 0.83. However, studies show that *Salmonella* can survive in foods with $a_w \ge 0.94$, reinforcing their ability to cause diseases even if present in a low number of cells. The number of *Salmonella* outbreaks related to foods with low a_w has been increasing each year, and the main foods involved are high-sugar-content products such as chocolate and honey smacks cereal, sesame seed-based products, peanut butter, and almonds (Alshammari et al., 2020) (Figure 1).

According to the EFSA, the most recent cases date from 2018 to 2021. An outbreak of *Salmonella* Poona involving a rice-based infant formula affected 30 people in France, one in Belgium, and one in Luxembourg. Symptoms were reported between August 2018 and February 2019 (EFSA, 2019b). In 2020, 124 cases of *Salmonella* Typhimurium and one of *S.* Anatum were reported, 105 in the United Kingdom (including the *S.* Anatum case), 14 in France, three in Luxembourg, and one each in the Netherlands and Canada. The vehicles of infection were nut products imported from Brazil and Bolivia (EFSA, 2020). Between January 2019 and October 2021, a total of 121 contamination

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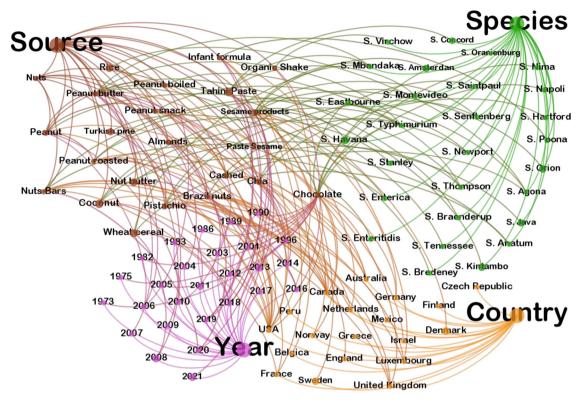


FIGURE 1 Outbreaks caused by *Salmonella* sp. related to low-water-activity foods around the world. This image contains the relationship between the *Salmonella* serotype, the food involved, the country, and the year of occurrence of the outbreak. **References**: CDC, 2004, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2016a, 2016b, 2016c, 2017, 2018a, 2018b, 2018c, 2019a, 2019b; Craven et al., 1975; D'Aoust et al., 1975; EFSA, 2017, 2019b, 2020, 2021; Elton, 2006; Gill et al., 1983; Greenwood & Hooper, 1983; Harvey et al., 2017; Hockin et al., 1989; Kapperud et al., 1990; Killalea et al., 1996; Kirk et al., 2004; Scheil et al., 1998; Werber et al., 2005

cases of sesame-based products from Syria were described in Sweden, Germany, Denmark, Norway, and the Netherlands, being *S*. Havana, *S*. Orion, *S*. Amsterdan, *S*. Mbandaka, *S*. Kintambo, and *S*. Senftenberg the reported serotypes. Children under 10 were the most affected (EFSA, 2021).

In-depth research in government agencies such as Centers for Disease Control and Prevention (CDC), European Food Safety Authority (EFSA), and Food and Drug Administration (FDA) showed no recent cases of salmonellosis in low-moisture foods. However, according to FDA (2022), in the United States four recalls were reported in March, May, August, and November 2021, involving hummus, nut flour, potato chips, and tahini, respectively.

2.5 | Survival mechanisms and thermoresistance of *Salmonella* in foods with low water activity

Several factors influence the vulnerability of a microorganism, such as intrinsic (a_w , humidity, pH, solids, acids, and fat content) and extrinsic (temperature, chemical, and gas composition) food factors, even the characteristics of the isolate (serotypes and growth phase) (Rolfe & Daryaei, 2020).

The low a_w of a food causes a condition called osmotic stress, creating an unfavorable environment for *Salmonella*, which must develop strategies to survive. One important example of mechanism is the osmoregulation that allows the bacteria to balance its internal composition with the external environment when subjected to a lowwater-activity condition, causing the accumulation of compatible solutes such as proline, glycinebetaine, ectoine, and trehalose to reduce water loss (Burgess et al., 2016). In addition, osmoregulation maintains the bacteria's turgor pressure (Bremer & Krämer, 2019).

Dormancy is another strategy. *Salmonella* enters the viable but nonculturable (VBNC) state when exposed to stressful environmental changes, not being able to develop in that place, but still alive. When conditions are again favorable, these cells return to a normal metabolic state (Highmore et al., 2018; Salive et al., 2020).

Cross-protection or cross-tolerance is also observed in *Salmonella*. The bacteria become resistant to stress conditions such as desiccation, osmotic stress, chemical (presence of ethanol and hypochlorite of sodium), and physical stresses (UV light irradiation and heat used during food processing) (Gruzdev et al., 2011; Finn et al., 2013). This tolerance can be attributed to inadequate sanitation practices, ineffective development of equipment, and failures in control and storage of ingredients, which reinforce *Salmonella*'s ability to survive for long periods in these foods and also on surfaces (Podolak & Black, 2017; Grasso et al., 2015).

The high fat content of certain foods, such as peanut butter and chocolates, may also affect the pathogen's survival, as the fat protects bacterial cells against the effects of gastric acid, allowing colonization of the gastrointestinal tract and the consequent production of clinical signs (Olaimat et al., 2020).

The osmotic stress can also modify important components of the pathogen's cell membrane like fatty acid and phospholipids. Chen et al. (2014) showed that, after 14 days of *Salmonella* exposure to foods with low a_w , an increased expression of *fabA* gene was related to the increased bacterial survival in that environment. However, it is still necessary to develop further studies focused on the role of those membrane modifications, composition, and how it affects *Salmonella* survival.

Microorganisms are constantly adapting, and there may be changes in their physiology and genetic behavior to support extreme physical conditions (Aguirre-Sanchez et al., 2021). Thermal shock enables the production of proteins (Hsp70, GroEL, DnaK, GrpE, etc.) that allow the bacteria to survive better in adverse conditions, and even participates in adhesion and invasion processes. The synthesis and expression of these proteins is not only influenced by heat stress, but also by changes in osmotic pressure, ultraviolet radiation, presence of salts of heavy metals, oxygen and peroxides radicals, and acid and oxidative stresses, a fact that may be relevant to understand bacterial protection against heat (Fourie & Wilson, 2020; Kurashova, Madaeva & Kolesnikova, 2020; Kim et al., 2021).

Abdelhamid and Yousef (2020) suggested that *Salmonella* biofilm may also contribute to desiccation survival thanks to its extracellular polymeric structure, which creates a protective and favorable microenvironment. Structures such as fimbriae and cellulose can contribute to *Salmonella* survival against desiccation stress; however, information about the production of biofilm in response to desiccation stress is still scarce.

In addition to all the mechanisms mentioned, several studies demonstrate the ability of *Salmonella* to develop the so-called thermoresistance, which, for Podolak et al. (2010), occurs mainly due to the capacity of bacterial cells to reduce their metabolism under unfavorable conditions and resume it when its growth is favored. Heat resistance

is a characteristic that can be acquired by *Salmonella* when they are exposed to the stress conditions of the low-wateractivity environment, allowing the bacteria to undergo adaptations that result in their persistence and survival (Chen & Jiang, 2017; Cui et al., 2019).

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According to Dawoud et al. (2017), the survival of *Salmonella* during thermal processing can be explained by several factors. One is that the microorganism has an increased ability to survive when pre-exposed to stressful conditions before the food undergoes heat treatments. Stressed cells, whether by heat, low-carbon sources, desiccation, or starvation stress, tend to have greater tolerance to thermal treatments.

The bacterial adaptation to stressful environment occurs through thermosensors, which are cellular structures (lipids, proteins, DNAs, and RNAs) capable of perceiving internal temperature fluctuations, and inducing the expression of adaptive and protective genes (Narayan et al., 2017; Loh et al., 2018). Sigma factors are a group of genes expressing proteins that organize the transcriptional activities related to stress responses. Sigma factor $\sigma^{\rm E}$ protects the cell against stress oscillation and regulates extracellular responses, and $\sigma^{\rm H}$ regulates cytoplasmic response to thermal stresses by the transcription of heat shock genes. RpoS is another example, acting mainly in the expression of proteins and in virulence genes regulation (Bhunia, 2018; Kang et al., 2018; Mutz et al., 2019).

The exposure of *Salmonella* to heat treatments can also stimulates the expression of virulence genes (Fong & Wang, 2016). To tolerate thermal stress, the first cell response is the expression of genes related to stress and energetic metabolism. However, this can culminate in cross-resistance to several other types of stresses, thus increasing its virulence potential, either through fimbriae expression, increased capacity of adhesion, or survival within the host (Sirsat et al., 2011; Aviles et al., 2013).

The use of heat treatments in the industry aims to ensure food safety, as temperatures around 70°C inactivate most enzymes and microorganism's vegetative cells (Ferrández et al., 2018; Huang, 2019). However, studies have shown that heat penetration does not occur homogeneously in the food, not being able to eradicate all contamination (Adepoju et al., 2016; Aboud et al., 2019).

In structural terms, the effect of desiccation on the thermal resistance of *Salmonella* has not been fully described. Studies suggest an intimate relationship between microbial survival and water mobility. Heat treatments cause water evaporation, triggering structural weakening of cell membranes and intracellular protein denaturation. However, the absence of water in low-moisture foods ends up playing a protective effect on cellular protein denaturation caused by high temperatures. Furthermore, the protection

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of noncoding DNA and RNAs also influences the response again desiccation (Lian, et al., 2015; Maserati et al., 2018; Gautan et al., 2020; Xu et al., 2020).

2.6 | Control of *Salmonella* in foods with low water activity

The high capacity of *Salmonella* to adapt to adverse environmental conditions brings the need for effective control measures for its eradication (Pradhan & Devi Negi, 2019). Validation of a monitoring system is essential to ensure microbial safety and to track the level of hygiene and efficacy of cleaning in production environments (Bourdichon et al., 2021). In the United States, the food industry mitigates and controls hazards by implementing and validating mandatory processing by the Food Safety Modernization Act (FMSA) according to the FDA (Wason et al., 2021). However, process validation should be rigorous, since studies with planktonic cells do not have the same efficiency for biofilm control (Xu et al., 2022).

The microenvironment in which the bacteria is inserted influences the increase or decrease in its sensitivity to thermal treatments over time (Jin, Tang & Zhu, 2020). Many microorganisms, pathogenic or not, can survive drying processes and this represents one of the main challenges in the food production, especially those with low a_w (Chitrakar, Zhang & Adhikari, 2018).

When food is subjected to a change in temperature, its a_w also changes. This happens thanks to food composition and food characteristics such as physical and physicochemical conditions. So, it is important to assess the difference in values of a_w depending on the heat treatment that is used to compare the effectiveness of those treatments. However, current information on the response of food to heat treatments and the consequent change in its a_w values is limited and cannot yet be predicted (Syamaladevi et al., 2016a, 2016b).

2.6.1 | Innovator studies on inhibition of *Salmonella* in foods with low water activity

There is currently little information about effective measures to control *Salmonella* specifically in low-wateractivity food matrices probably because they are more heat tolerant than in aqueous food matrices (Xu et al., 2019). However, several studies have emerged reporting the use of different techniques to try to control these microorganisms. One example is a new approach by growth curve analysis to distinguish between antimicrobial and antibiofilm activities against *Salmonella* simply and quickly, which allows testing a greater number of active compounds against this species (Sterniša et al., 2022). Liu et al. (2018) point out the antibacterial role of SiO_2 , being able to naturally dehydrate bacterial cells, but this technique needs to be better studied.

Radiofrequency (RF) is a new technology in food processing research for drying, sterilizing, disinfecting, and cooking through the conversion of electrical energy into thermal energy, affecting the migration of microparticles (Tong et al., 2022). RF energy (27.12 MHz, 6 kW) reduced 5 log CFU/g of *Salmonella* in cumin seeds (Chen et al., 2020) and also in spices without affecting color (Ozturk et al., 2020). *Salmonella* Typhimurium was also reduced by RF heating for red pepper powder (Jiao et al, 2021).

The use of ionizing radiation like X-ray, gamma-ray, and electron-beam irradiation represents an alternative to microbial inactivation in some foods. This technology is able to minimize pathogenic and spoilage microorganisms and still unchanging the food quality (Pi et al., 2021). Steinbrunner et al (2019) observed in almond products, date, and wheat that *Salmonella* resistance to X-ray irradiation increased with increasing food a_w . The fact that these foods have gone through processes that changed their physical structure reflected in the bacteria's resistance, which was reduced. However, there is no previously reported relation-ship between bacterial resistance to radiation and structural food changes.

Essential oils (EOs) are natural alternatives of food preservatives and antimicrobial agents, since the demand for replacing synthetic compounds is a reality nowadays (Ed-Dra et al, 2021). Olaimat et al (2018) and Al-Nabulsi et al (2020) showed the effectiveness of AITC (allyl isothiocyanate) in hummus and of cinnamon and thyme oils in tahini, respectively. However, further studies involving EOs and a greater variety of low-water-activity foods are needed, as well as exploring ways to avoid possible changes in food taste and odor.

Chemical compounds such as acetic and citric acids also represent control alternatives, since the pH of these compounds is lower than the optimal pH that *Salmonella* supports to grow (Maduchanka et al, 2018). Both acids are potent antimicrobial agents and their use in food is considered safe (Olaimat et al., 2017). Al-Nabulsi et al (2014) showed reduced viability of *Salmonella* Typhimurium in tahini. This treatment can also be better explored for other foods with low a_w due to its scarcity in the literature.

The union of mathematical and microbiological concepts allowed the development of faster and more reliable solutions to quantitatively measure microbial behavior during inactivation process. Predictive models assume that microbial behavior can be reproducible in face of environmental changes, such as those caused by heat treatment (Stavropoulou & Bezirtzoglou, 2019). These models can be linear and nonlinear: linear models describe that the entire bacterial population has equal thermal sensitivity and identical probability of death, while nonlinear ones address microbial behavior during inactivation from different curvature models (Evelyn & Silva, 2020; Buzrul, 2022).

The Weibull model is an important parameter that helps to determine *Salmonella* inactivation kinetics, used in both linear and nonlinear examples (Jiao et al., 2019). Considering the repetitive exposure of microorganisms to dangerous conditions and environments, the Weibull model, then, establishes the survival rate of this microbial population: if the concavity of the survival curve is upward, the population shows adaptation and medium/high resistance to induced stress; decreasing concavities lead to a reduction in the number of microorganisms (Serment-Moreno, 2020).

The association between biological and mathematical knowledge represents a fundamental output for the development of preventive control measures or even new strategies (Dementavicius et al., 2016; Tadapaneni et al., 2018; Kim et al., 2021). Information about genetic determinants and molecular mechanisms that allow *Salmonella* survival in these foods is still scarce, so it is extremely important to encourage further studies to combat this pathogen (Jayeola et al., 2020).

The so-called nonthermal decontamination technologies are currently gaining prominence for their ability to maintain the safety of foods with low a_w and to promote smaller changes in its final quality compared to heat treatments. They are cold plasma, pulsed light, ultraviolet light, and light-emitting diode (LED) (Deng et al, 2020).

Cold plasma consists of an ionized gas capable of affecting bacterial cell membrane and the subsequent reaction with DNA, RNA, and proteins (Hertrich et al., 2017; Mandal, Singh & Singh, 2018). This technology is mainly applied to meats, fruits, and vegetables (Chizoba Ekezie, Sun & Cheng, 2017), but effective cases of *Salmonella* reduction in black pepper (Sun et al., 2014) and shelled almonds (Hertwig et al., 2017) have been reported.

Pulsed light uses short-pulse but high-density lights with good antimicrobial capability. A capacitor is responsible for accumulating electrical energy and releasing it in the form of inert gases (Mahendran et al, 2019; Liu et al, 2021). This technology has brought good results in reducing *Salmonella* populations in chia seeds (Reyes-Jurado et al, 2019), dried parsley (Dittrich et al, 2021), almonds (Oner, 2017; Harguindeguy & Gómez-Camacho, 2021), and *Enterococcus faecium* (*Salmonella* Surrogate) in nonfat dry milk, wheat flour, and egg white powder (Chen et al, 2019).

Ultraviolet (UV) light is a potent technology for surface decontamination and has a lethal nature by promoting damage to microbial DNA (Kaavya et al, 2021). It has shown positive results in inactivating *Salmonella* in wheat flour (Códon-Abanto et al, 2016), shelled walnuts (Izmirli-

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oglu & Demirci, 2018), and black peppercorns (Xie & Hung, 2020). Alone or combined with UV light, LED is also a promising technology characterized by release of energy in the form of light (Prasad, Ganzle & Roopesh, 2019). Like the others, it was effective in decontaminating *Salmonella* in wheat flour (Du et al, 2019; Subedi et al, 2020).

3 | CONCLUSION

Salmonella pathogenicity can be widely expressed through virulence factors, in addition to several mechanisms that contribute to its high capacity to adapt and survive in unfavorable environments and conditions, such as low-wateractivity foods and all the processes responsible for their production.

Given the epidemiological importance of this pathogen within the context of foodborne disease, it is necessary to establish and comply with adequate sanitary practices, as well as the creation of control measures that ensure the quality of foods with low a_w . In-depth knowledge about the response to the cellular stress that leads to bacterial persistence is also vital to understanding the risks of food contamination. The molecular basis of *Salmonella* in these foods may contribute on the development of inactivation and detection strategies.

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AUTHOR CONTRIBUTIONS

R.M.M. wrote the original draft. V.L.M.R. administered the project. S.T.A.D. reviewed and edited the manuscript. V.P.P.A. performed formal analysis. N.C.C.S. performed supervision.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

- Abdelhamid, A. G., & Yousef, A. E. (2020). Collateral adaptive responses induced by desiccation stress in *Salmonella enterica*. *Food Science and Technology*, *133*, 110089. https://doi.org/10.1016/ j.lwt.2020.110089
- Aboud, S. A., Altemimi, A. B., Al-HiIphy, A. R. S., Yi-Chen, L., & Cacciola, F. (2019). A comprehensive review on infrared heating applications in food processing. *Molecules*, *24*(22), 4125. https:// doi.org/10.3390/molecules24224125

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- Adepoju, M. A., Omitoyin, B. O., Mohan, C. O., & Zynudheen, A. A. (2016). Heat penetration attributes of milkfish (*Chanoschanos*) thermal processed in flexible pouches: a comparative study between steam application and water immersion. *Food Science & Nutrition*, 5, 521–524. https://doi.org/10.1002/fsn3.426
- Aguirre-Sanchez, J. R., Ibarra-Rodriguez, J. R., Vega-Lopez, I. F., Martínez-Urtaza, J., & Chaidez-Quiroz, C. (2021). Genomic signatures of adaptation to natural settings in non-typhoidal *Salmonella enterica* Serovars Saintpaul, Thompson and Weltevreden. Infection, Genetics and Evolution, 90, 104771. https://doi.org/10.1016/ j.meegid.2021.104771
- Al-Nabulsi, A. A., Olaimat, A. N., Osaili, T. M., Shaker, R. R., Elabedeen, N. Z., Jaradat, Z. W., Abushelaibi, A., & Holley, R. A. (2014). Use of acetic and citric acids to control *Salmonella* Typhimurium in tahini (sesame paste). *Food Microbiology*, *42*, 102– 108. https://doi.org/10.1016/j.fm.2014.02.020
- Al-Nabulsi, A. A., Osaili, T. M., Olaimat, A. N., Almasri, W. E., Ayyash, M., Al-Holy, M. A., Jaradat, Z. W., Obaid, R. S., & Richard, A. (2020). Inactivation of *Salmonella* spp. in tahini using plant essential oil extracts. *Food Microbiology*, *86*, 103338. https://doi. org/10.1016/j.fm.2019.103338
- Alshammari, J., Xu, J., Tang, J., Sablani, S., & Zhu, M.-J. (2020). Thermal resistance of *Salmonella* in low-moisture high-sugar products. *Food Control*, 114, 107255. https://doi.org/10.1016/j.foodcont.2020. 107255
- Ashenafi, M. (2012). Thermal effects in food microbiology. In D.-W. Sun (Ed.), *Thermal food processing: New technologies and quality issues* (2nd ed., pp. 65–80). CRC Press.
- Aviles, B., Klotz, C., Smith, T., Williams, R., & Ponder, M. (2013). Survival of *Salmonella enterica* serotype Tennessee during simulated gastric passage is improved by low water activity and high fat content. *Journal of Food Protection*, *76*(2), 333–337. https://doi.org/10. 4315/0362-028x.jfp-12-280
- Barbosa-Cánovas, G. V., Fontana, A. J., Jr., Schmidt, S. J., & Labuza, T. P. (Eds.). (2020). Water activity in foods: Fundamentals and applications. John Wiley & Sons.
- Bhunia, A. K. (2018). Salmonella enterica. In Foodborne microbial pathogens (pp. 271–287). Springer. https://doi.org/10.1007/978-1-4939-7349-1_15
- Blessington, T., Mitcham, E. J., & Harris, L. J. (2012). Survival of Salmonella enterica, Escherichia coli O157:H7, and Listeria monocytogenes on inoculated walnut kernels during storage. Journal of Food Protection, 75(2), 245–254. https://doi.org/10.4315/0362-028X. JFP-11-278
- Bourdichon, F., Betts, R., Dufour, C., Fanning, S., Farber, J., McClure, P., Stavropoulou, D. A., Wemmenhove, E., Zwietering, M. H., & Winkler, A. (2021). Processing environment monitoring in low moisture food production facilities: Are we looking for the right microorganisms? *International Journal of Food Microbiology*, 356, https://doi.org/10.1016/j.ijfoodmicro.2021.109351
- Brar, P. K., Proano, L. G., Friedrich, L. M., Harris, L. J., & Danyluk, M. D. (2015). Survival of *Salmonella*, *Escherichia coli* O157:H7, and *Listeria monocytogenes* on raw peanut and pecan kernels stored at -24, 4, and 22°C. *Journal of Food Protection*, 78(2), 323–332. https: //doi.org/10.4315/0362-028X.JFP-14-327
- Bremer, E., & Krämer, R. (2019). Responses of microorganisms to osmotic stress. *Annual Review of Microbiology*, 73(1), https://doi. org/10.1146/annurev-micro-020518-115504

- Burgess, C. M., Gianotti, A., Gruzdev, N., Holah, J., Knochel, S., Lehner, A., Marges, E., Esser, S. S., Sela, S., & Tresse, O. (2016). The response of foodborne pathogens to osmotic and desiccation stresses in the food chain. *International Journal of Food Microbiol*ogy, 221, 37–53. https://doi.org/10.1016/j.ijfoodmicro.2015.12.014
- Burnett, S. L., Gehm, E. R., Weissinger, W. R., & Beuchat, L. R. (2000). Survival of *Salmonella* in peanut butter and peanut butter spread. *Journal of Applied Microbiology*, *89*(3), 472–477. https://doi.org/10. 1046/j.1365-2672.2000.01138.x
- Buzrul, S. (2022). The Weibull model for microbial inactivation. *Food Engineering Reviews*, 14, 45–61. https://doi.org/10.1007/s12393-021-09291-y
- Čabarkapa, I., Čolović, R., Đuragić, O., Popović, S., Kokić, B., Milanov, D., & Pezo, L. (2019). Anti-biofilm activities of essential oils rich in carvacrol and thymol against *Salmonella* Enteritidis. *Biofouling*, 1–15. https://doi.org/10.1080/08927014.2019.1610169
- Carrasco, E., Morales-Rueda, A., & Garcia-Gimeno, R. M. (2012). Cross-contamination and recontamination by Salmonella in foods: A review. Food Research International, 45, 545–556. https:// doi.org/10.1016/j.foodres.2011.11.004
- Centers for Disease Control and Prevention (CDC). (2004). *Outbreak* of Salmonella serotype Enteritidis infections associated with raw almonds - United States and Canada, 2003–2004. https://www.cdc. gov/mmwr/preview/mmwrhtml/mm5322a8.html
- Centers for Disease Control and Prevention (CDC). (2007). Multistate outbreak of Salmonella serotype Tennessee infections associated with peanut butter – United States, 2006–2007, 2007. Morbidity and Mortality Weekly Report, 56(21), 521–524.
- Centers for Disease Control and Prevention (CDC). (2008). Multistate outbreak of Salmonella Agona infections linked to rice and wheat puff cereal (Final update). https://www.cdc.gov/salmonella/2008/ rice-wheat-puff-cereal-5-13-2008.html
- Centers for Disease Control and Prevention (CDC (2009). Multistate outbreak of Salmonella Typhimurium infections linked to peanut butter, 2008–2009. http://www.cdc.gov/salmonella/ typhimurium/index.html
- Centers for Disease Control and Prevention (CDC). (2010). *OutbreakNet foodborne outbreak online database*. http://wwwn.cdc.gov/foodborneoutbreaks/Default.aspx
- Centers for Disease Control and Prevention (CDC). (2011). Multistate outbreak of human Salmonella Enteritidis infections linked to Turkish pine nuts (Final update). https://www.cdc.gov/salmonella/ 2011/pine-nuts-11-17-2011.html
- Centers for Disease Control and Prevention (CDC). (2012). Multistate outbreak of Salmonella Bredeney infections linked to peanut butter manufactured by Sunland, Inc. (Final update). https://www.cdc. gov/salmonella/bredeney-09-12/index.html
- Centers for Disease Control and Prevention (CDC). (2013). Multistate outbreak of Salmonella Montevideo and Salmonella Mbandaka infections linked to tahini sesame paste (Final update). https://www.cdc.gov/salmonella/montevideo-tahini-05-13/
- Centers for Disease Control and Prevention (CDC). (2014). Multistate outbreak of Salmonella Braenderup infections linked to nut butter manufactured by spired natural foods. http://www.cdc.gov/ salmonella/braenderup-08-14/.Accessed
- Centers for Disease Control and Prevention (CDC). (2016). *What is salmonellosis*? http://www.cdc.gov/salmonella/general/index. html

- Centers for Disease Control and Prevention (CDC). (2016a). Multistate outbreak of Salmonella Virchow infections linked to garden of life raw meal organic shake & meal products. http://www.cdc.gov/ salmonella/virchow-02-16/index.html
- Centers for Disease Control and Prevention (CDC). (2016b). Multistate outbreak of Salmonella Montevideo and Salmonella Senftenberg infections linked to wonderful pistachios. http://www.cdc.gov/ salmonella/montevideo-03-16/.Accessed
- Centers for Disease Control and Prevention (CDC). (2016c). Multistate outbreak of Salmonella Paratyphi B variant L (+) tartrate (+) infections linked to JEM raw brand sprouted nut butter spreads (Final update). https://www.cdc.gov/salmonella/paratyphi-b-12-15/index.html
- Centers for Disease Control and Prevention (CDC). (2017). Foodborne outbreak online database – Salmonella (1998–2015). https://wwwn. cdc.gov/foodborneoutbreaks/
- Centers for Disease Control and Prevention (CDC). (2018a). Multistate outbreak of Salmonella infections linked to coconut tree brand frozen shredded coconut (Final update). https://www.cdc. gov/salmonella/coconut-01-18/index.html
- Centers for Disease Control and Prevention (CDC). (2018b). Multistate outbreak of Salmonella Typhimurium infections linked to dried coconut (Final update). https://www.cdc.gov/salmonella/ typhimurium-03-18/index.html
- Centers for Disease Control and Prevention (CDC). (2018c). Multistate outbreak of Salmonella Mbandaka infections linked to Kellogg's honey smacks cereal (Final update). https://www.cdc.gov/ salmonella/mbandaka-06-18/index.html
- Centers for Disease Control and Prevention (CDC). (2019a). Outbreak of Salmonella infections linked to tahini from Achdut Ltd. https:// www.cdc.gov/salmonella/concord-11-18/index.html
- Centers for Disease Control and Prevention (CDC). (2019b). Outbreak of Salmonella infections linked to Karawan brand tahini. https:// www.cdc.gov/salmonella/concord-05-19/index.html
- Chen, W., Golden, D. A., & Critzer, F. J. (2014). Salmonella survival and differential expression of fatty acid biosynthesis-associated genes in a low-water-activity food. *Letters in Applied Microbiology*, 59, 133–138. https://doi.org/10.1111/lam.12253
- Chen, Z., & Jiang, X. (2017). Thermal resistance and gene expression of both desiccation-adapted and rehydrated Salmonella enterica serovar Typhimurium cells in aged broiler litter. Applied and Environmental Microbiology, 83(12), https://doi.org/10.1128/aem. 00367-17
- Chen, D., Cheng, Y., Peng, P., Liu, J., Wang, Y., Ma, Y., Anderson, E., Chen, C., Chen, P., Ruan, R., & Ruan, R. (2019). Effects of intense pulsed light on *Cronobacter sakazakii* and *Salmonella* surrogate *Enterococcus faecium* inoculated in different powdered foods. *Food Chemistry*, 296, 23–28. https://doi.org/10.1016/j.foodchem.2019.05. 180
- Chen, L., Irmak, S., Chaves, B. D., & Subbiah, J. (2020). Microbial challenge study and quality evaluation of cumin seeds pasteurized by continuous radio frequency processing. *Food Control*, 111, 107052. https://doi.org/10.1016/J.FOODCONT.2019.107052
- Chitrakar, B., Zhang, M., & Adhikari, B. (2018). Dehydrated foods: Are they microbiologically safe? *Critical Reviews in Food Sci*ence and Nutrition, 1–12. https://doi.org/10.1080/10408398.2018. 1466265
- Ekezie, C. F-G., Sun, D-W., & Cheng, J.-H (2017). A review on recent advances in cold plasma technology for the food industry: Current

applications and future trends. *Trends in Food Science & Technology*, 69, 46–58. https://doi.org/10.1016/j.tifs.2017.08.007

Food Science Willey-

- Christidis, T., Hurst, M., Rudnick, W., Pintar, K. D. M., & Pollari, F. (2020). A comparative exposure assessment of foodborne, animal contact and waterborne transmission routes of *Salmonella* in Canada. *Food Control*, 109, 106899. https://doi.org/10.1016/j. foodcont.2019.106899
- Condón-Abanto, S., Condón, S., Raso, J., Lyng, J. G., & Álvarez, I. (2016). Inactivation of Salmonella Typhimurium and Lactobacillus plantarum by UV-C light in flour powder. Innovative Food Science & Emerging Technologies, 35, 1–8. https://doi.org/10.1016/j. ifset.2016.03.008
- Craven, P. C., Baine, W., Mackel, D., Barker, W., Gangarosa, E., Goldfield, M., Rosenfeld, H., Altman, R., Lachapelle, G., Davies, J. W., & Swanson, R. C. (1975). International outbreak of *Salmonella* Eastbourne infection traced to contaminated chocolate. *The Lancet*, 1(7910), 788–793. https://doi.org/10.1016/s0140-6736(75)92446-0
- Crucello, A., Furtado, M. M., Chaves, M. D. R., & Sant'ana, A. S. (2019). Transcriptome sequencing reveals genes and adaptation pathways in *Salmonella* Typhimurium inoculated in four low water activity foods. *Food Microbiology*, 82, 426–435. https://doi. org/10.1016/j.fm.2019.03.016
- Cui, X., Hu, C., Ou, L., Kuramitsu, Y., Masuda, Y., Honjoh, K., & Miyamoto, T. (2019). Transcriptional analysis on heat resistance and recovery from thermal damage in *Salmonella* under high salt condition. *LWT Food Science and Technology*, *106*, 194–200. https: //doi.org/10.1016/j.lwt.2019.02.056
- D'Aoust, J. Y., Aris, B. J., Thisdele, P., Durante, A., Brisson, N., Dragon, D., Lachapekke, G., Johnston, M., & Laidley, R. (1975). Salmonella Eastbourne outbreak associated with chocolate. *Canadian Institute of Food Science and Technology Journal*, 8(4), 181– 184. https://doi.org/10.1016/S0315-5463(75)73804-X
- Dawoud, T. M., Davis, M. L., Park, S. H., Sun, A. K., Kwon, Y. M., & Ricke, S. C. (2017). The potential link between thermal resistance and virulence in *Salmonella*: A review. *Frontiers in Veterinary Science*, 4, 93. https://doi.org/10.3389/fvets.2017.00093
- Dementavicius, D., Lukseviciute, V., Gómez-López, V. M., & Luksiene, Z. (2016). Application of mathematical models for bacterial inactivation curves using Hypericin-based photosensitization. *Journal of Applied Microbiology*, *120*(6), 1492–1500. https://doi.org/ 10.1111/jam.13127
- Deng, L.-Z., Tao, Y., Mujumdar, A. S., Pan, Z., Chen, C., Yang, D.-H., Liu, Z.-L., Wang, H., & Xiao, H.-W. (2020). Recent advances in non-thermal decontamination technologies for microorganisms and mycotoxins in low-moisture foods. *Trends in Food Science & Technology*, *106*, 104–112. https://doi.org/10.1016/j.tifs.2020.10.012
- Dittrich, A. J., Ludewig, M., Rodewald, S., Braun, P. G., & Wiacek, C. (2021). Pulsed-light treatment of dried parsley: reduction of artificially inoculated *Salmonella* and impact in given quality parameters. *Journal of Food Protection*, *84*(8), 1421–1432. https://doi.org/ 10.4315/JFP-20-469
- Dos Santos, A. M. P., Ferrari, R. G., Panzenhagen, P., Rodrigues, G. L., & Conte-Junior, C. A (2021). Virulence genes identification and characterization revealed the presence of the *Yersinia* High Pathogenicity Island (HPI) in *Salmonella* from Brazil. *Gene*, 787, 145646. https://doi.org/10.1016/j.gene.2021.145646
- Du, L., Prasad, J. A., Ganzle, M., & Roopesh, M. S. (2019). Inactivation of *Salmonella* spp. in wheat flour

WILEY Food Science

by 395 nm pulsed light emitting diode (LED) treatment and the related functional and structural changes of gluten. *Food Research International*, *127*, 108716. https:// doi.org/10.1016/j.foodres.2019.108716

- Ed-Dra, A., Nalbone, L., Filali, F. R., Trabelsi, N., El Majdoub, Y. O., Bouchrif, B., Giarratana, F., & Giuffrida, A. (2021). Comprehensive evaluation on the use of *Thymus vulgaris* essential oil as natural additive against different serotypes of Salmonella enterica. *Sustainability*, *13*(8), 4594. https://doi.org/10.3390/su13084594
- European Food Safety Authority (EFSA). (2017). Multi-country outbreak of new Salmonella Enterica 11:z41:e,n,z15 infections associated with sesame seeds. https://doi.org/10.2903/sp.efsa.2017.EN-1256
- European Food Safety Authority (EFSA). (2019a). *The European* Union One Health 2018 Zoonoses Report. ECDC/EFSA. https://doi. org/10.2903/j.efsa.2019.5926
- European Food Safety Authority (EFSA). (2019b). Multi-country outbreak of Salmonella Poona infections linked to consumption of infant formula. ECDC/EFSA. https://doi.org/10.2903/sp.efsa.2019. EN-1594
- European Food Safety Authority (EFSA). (2020). *Multi-country outbreak of* Salmonella *Typhimurium and* S. *Anatum infections linked to Brazil nuts.* ECDC/EFSA. https://doi.org/10.2903/sp.efsa.2020. EN-1944
- European Food Safety Authority (EFSA). (2021). Multi-country outbreak of multiple Salmonella enterica serotypes linked to imported sesame-based products. ECDC/EFSA. https://doi.org/10.2903/sp. efsa.2021.EN-6922
- Elton, R. (2006). National increase in human Salmonella Montevideo infections in England and Wales: March to June 2006. Euro Surveillance, 11(26), 2985. https://doi.org/10.2807/esw.11.26.02985en
- Enache, E., Podolak, R., Kataoka, A., & Harris, L. J. (2017). Persistence of Salmonella and other bacterial pathogens in low-moisture foods. Control of Salmonella and Other Bacterial Pathogens in Low Moisture Foods, 67–86. https://doi.org/10.1002/9781119071051.ch4
- Espinoza, R. A., Silva-Valenzuela, C. A., Amaya, F. A., Urrutia, Í. M., Contreras, I., & Santiviago, C. A. (2017). Differential roles for pathogenicity islands SPI-13 and SPI-8 in *Salmonella* Enteritidis and *Salmonella* Typhi with murine and human macrophages. *Biological Research*, 50(1), 5. https://doi.org/10.1186/s40659-017-0109-8
- Evelyn, E., & Silva, F. V. M. (2020). Ultrasound assisted thermal inactivation of spores in foods: Pathogenic and spoilage bacteria, molds and yeasts. *Trends in Food Science & Technology*, 105, 402–415. https://doi.org/10.1016/j.tifs.2020.09.020
- Farakos, S. M. S., Frank, J. F., & Schaffner, D. W. (2013). Modeling the influence of temperature, water activity and water mobility on the persistence of *Salmonella* in low-moisture foods. *International Journal Food Microbiology*, *166*, 280–293. https://doi.org/10.1016/j. ijfoodmicro.2013.07.007
- Fardsanei, F., Dallal, M. M. S., Douraghi, M., Memariani, H., Bakhshi, B., Salehi, T. Z., & Nikkhahi, F. (2018). Antimicrobial resistance, virulence genes and genetic relatedness of *Salmonella enterica* serotype Enteritidis isolates recovered from human gastroenteritis in Tehran, Iran. *Journal of Global Antimicrobial Resistance*, 12, 220–226. https://doi.org/10.1016/j.jgar.2017.10.005
- FDA (2022). Recalls, Market Withdrawals, & Safety Alerts. Food and Drug Administration (FDA). https://www.fda.gov/safety/recallsmarket-withdrawals-safety-alerts

- Ferrández, M. R., Puertas-Martín, S., Redondo, J. L., Ivorra, B., Ramos, A. M., & Ortigosa, P. M. (2018). High-performance computing for the optimization of high-pressure thermal treatments in food industry. *The Journal of Supercomputing*, 75, 1187–1202. https://doi.org/10.1007/s11227-018-2351-4
- Ferrari, R. G., Rosario, D. A., Cunha-Neto, A., Mano, S. B., Figueiredo, E. E. S., & Conte-Junior, C. A. (2019). Worldwide Epidemiology of *Salmonella* Serovars in Animal-Based Foods: a Meta-analysis. *Applied and Environmental Microbiology*, 85(14), e00591–19. https://doi.org/10.1128/AEM.00591-19
- Finn, S., Condell, O., McClure, P., Amezquita, A., & Fanning, S. (2013). Mechanisms of survival, responses and sources of *Salmonella* in low-moisture environments. *Frontiers in Microbiol*ogy, 4, 331. https://doi.org/10.3389/fmicb.2013.00331
- Fong, K., & Wang, S. (2016). Heat resistance of Salmonella enterica is increased by pre-adaptation to peanut oil or sub-lethal heat exposure. Food Microbiology, 58, 139–147. https://doi.org/10.1016/j.fm. 2016.04.004
- Fourie, K. R., & Wilson, H. L. (2020). Understanding GroEL and DnaK Stress Response Proteins as Antigens for Bacterial Diseases. *Vaccines*, 8(4), 773. https://doi.org/10.3390/vaccines8040773
- Fowoyo, P. T. (2020). The mechanisms of virulence and antimicrobial resistance in Salmonella enterica serovar Typhi: A systematic review. African Journal of Biological Sciences, 2(4), 13–26. https://doi.org/10.33472/AFJBS.2.4.2020.13-26
- Garces-Vega, F. J., Ryser, E. T., & Marks, B. P. (2019). Relationships of water activity and moisture content to the thermal inactivation kinetics of *Salmonella* in low-moisture foods. *Journal of Food Protection*, *82*(6), 963–970. https://doi.org/10.4315/0362-028X.JFP-18-549
- Gautan, B., Govindan, B. N., Ganzle, M., & Roopesh, M. S. (2020). Influence of water activity on the heat resistance of *Salmonella enterica* in selected low-moisture foods. *International Journal of Food Microbiology*, 334, 108013. https://doi.org/10.1016/ j.ijfoodmicro.2020.108813
- Gill, O. N., Sockett, P. N., Bartlett, C. L., Vaile, M. S., Rowe, B., Gilbert, R. J., Dulake, C., Murrell, H. C., & Salmaso, S. (1983). Outbreak of *Salmonella* Napoli infection caused by contaminated chocolate bars. *The Lancet*, 321(8324), 574–577. https://doi.org/10.1016/s0140-6736(83)92822-2
- Grasso, E. M., Grove, S. F., Halik, L. A., Arritt, F., & Keller, S. E. (2015). Cleaning and sanitation of *Salmonella*-contaminated peanut butter processing equipment. *Food Microbiology*, 46, 100–106. https: //doi.org/10.1016/j.fm.2014.03.003
- Greenwood, M. H., & Hooper, W. L. (1983). Chocolate bars contaminated with Salmonella Napoli: an infectivity study. British Medical Journal, (Clinical Research ed.). 286, 6375. https://doi.org/10.1136/ bmj.286.6375.1394
- Gruzdev, N., Pinto, R., & Sela, S. (2011). Effect of desiccation on tolerance of Salmonella enterica to multiple stresses. Applied and Environmental Microbiology, 77(5), 1667–1673. https://doi.org/10.1128/ AEM.02156-10
- Harguindeguy, M., & Gómez-Camacho, C. E. (2021). Pulsed Light (PL) Treatments on Almond Kernels: Salmonella enteritidis Inactivation Kinetics and Infrared Thermography Insights. Food and Bioprocess Technology, 14, 2323–2335. https://doi.org/10.1007/ s11947-021-02725-9
- Harvey, R. R., Heiman Marshall, K. E., Burnworth, L., Hamel, M., Tataryn, J., Cutler, J., Meganth, K., Wellman, A., Irvin, K., Isaac, L.,

Chau, K., Locas, A., Kihl, J., Huth, P. A., Nicholas, D., Traphagen, E., Soto, K., Mank, L., Holmes-Talbot, K., & Gieraltowski, L. (2017). International outbreak of multiple *Salmonella* serotype infections linked to sprouted chia seed powder – USA and Canada, 2013–2014. *Epidemiology and Infection*, *145*(8), 1535–1544. https://doi.org/10.1017/S0950268817000504

- Hertrich, S. M., Boyd, G., Sites, J., & Niemira, B. A. (2017). Cold Plasma Inactivation of Salmonella in Prepackaged, Mixed Salads Is Influenced by Cross-Contamination Sequence. Journal of Food Protection, 80(12), 2132–2136. https://doi.org/10.4315/0362-028X.JFP-17-242
- Hertwig, C., Leslie, A., Meneses, N., Reineke, K., Rauh, C., & Schlüter, O. (2017). Inactivation of *Salmonella* Enteritidis PT30 on the surface of unpeeled almonds by cold plasma. *Innovative Food Science & Emerging Technologies*, 44, 242–248. https://doi.org/10. 1016/j.ifset.2017.02.007
- Highmore, C. J., Warner, J. C., Rothwell, S. D., Wilks, S. A., & Keevil, C. W. (2018). Viable-but-Non culturable *Listeria monocytogenes* and *Salmonella enterica* Serovar Thompson Induced by Chlorine Stress Remain Infectious. *mBio*, 9(2), e00540–18. https://doi.org/ 10.1128/mbio.00540-18
- Hockin, J. C., D'Aoust, J.-Y., Bowering, D., Jessop, J. H., Khanna, B., Lior, H., & Milling, M. E (1989). An International Outbreak of *Salmonella* Nima from Imported Chocolate. *Journal of Food Protection*, 52(1), 51–54. https://doi.org/10.4315/0362-028x-52.1.51
- Huang, L. (2019). Reconciliation of the D/z model and the Arrhenius model: The effect of temperature on inactivation rates of chemical compounds and microorganisms. *Food Chemistry*, 295, 499–504. https://doi.org/10.1016/j.foodchem.2019.05.15
- Ilyas, B., Tsai, C. N., & Coombes, B. K. (2017). Evolution of Salmonella-host cell interactions through a dynamic bacterial genome. Frontiers in Cellular and Infection Microbiology, 7, 428. https://doi.org/10.3389/fcimb.2017.00428
- Izmirlioglu, G., & Demirci, A. (2018). Inactivation of Salmonella Enteritidis on walnuts by pulsed UV treatment. American Society of Agricultural and Biological Engineers, 134, 110023. https://doi. org/10.13031/aim.201800334
- Jajere, S. M. (2019). A review of Salmonella enterica with particular focus on the pathogenicity and virulence factors, host specificity and antimicrobial resistance including multidrug resistance. Veterinary World, 12(4), 504–521. https://doi.org/10.14202/vetworld. 2019.504-521
- Jayeola, V., McClelland, M., Porwollik, S., Chu, W., Farber, J., & Kathariou, S. (2020). Identification of Novel Genes Mediating Survival of *Salmonella* on Low-Moisture Foods via Transposon Sequencing Analysis. *Frontiers in Microbiology*, 11, https://doi.org/ 10.3389/fmicb.2020.00726
- Jiao, S., Zhang, H., Hu, S., & Zhao, Y. (2019). Radio frequency inactivation kinetics of *Bacillus cereus* spores in red pepper powder with different initial water activity. *Food Control*, 105, 174–179. https:// doi.org/10.1016/j.foodcont.2019.05.038
- Jiao, S., Zhang, H., Liao, M., Hayouka, Z., & Jing, P. (2021). Investigation of the potential direct and cross protection effects of sublethal injured *Salmonella* Typhimurium induced by radio frequency heating stress. *Food Research International*, 150(A), 110789. https://doi.org/10.1016/j.foodres.2021.110789
- Jin, Y., Pickens, S. R., Hildebrandt, I. M., Burbick, S. J., Grasso-Kelley, E. M., Keller, S. E., & Anderson, N. M. (2018). Thermal inactivation of *Salmonella* Agona in low-water activity foods: predic-

tive models for the combined effect of temperature, water activity, and food component. *Journal of Food Protection*, *81*(9), 1411–1417. https://doi.org/10.4315/0362-028X.JFP-18-041

- Jin, Y., Tang, J., & Zhu, M.-J. (2020). Water Activity Influence on the Thermal Resistance of *Salmonella* in Soy Protein Powder at Elevated Temperatures. *Food Control*, 107160. https://doi.org/10.1016/ j.foodcont.2020.10716
- Jung, Y. S., & Beuchat, L. R. (1998). Survival of multidrug-resistant Salmonella typhimurium DT104 in egg powders as affected by water activity and temperature. International Journal of Food Microbiology, 49(1-2), 1–8. https://doi.org/10.1016/s0168-1605(99) 00013-6
- Kaavya, R., Pandiselvam, R., Abdullah, S., Sruthi, N. U., Jayanath, Y., Ashokkumar, C., Khanashyam, A. C., Kothakota, A., & Ramesh, S. V. (2021). Emerging non-thermal technologies for decontamination of *Salmonella* in food. *Trends in Food Science & Technology*, *112*, 400–418. https://doi.org/10.1016/j.tifs.2021.04.011
- Kang, I.-B., Kim, D.-H., Jeong, D., Park, J.-H., & Seo, K.-H. (2018). Heat resistance of *Salmonella Enteritidis* under prolonged exposure to acid-salt combined stress and subsequent refrigeration. *International Journal of Food Microbiology*, 285, 165–172. https:// doi.org/10.1016/j.ijfoodmicro.2018.08
- Kapperud, G., Gustavsen, S., Hellesnes, I., Hansen, A. H., Lassen, J., Hirn, J., Jahkola, M., Montenegro, M. A., & Helmuth, R. (1990). Outbreak of *Salmonella* Typhimurium infection trace to contaminated chocolate and caused by a strain lacking the 60-megadalton virulence plasmid. *Journal of Clinical Microbiology*, 28(12), 2597– 2601. https://doi.org/10.1128/jcm.28.12.2597-2601.1990
- Kataoka, A., Enache, E., Black, D. G., Elliott, P. H., Napier, C. D., Podolak, R., & Hayman, M. M. (2014). Survival of Salmonella Tennessee, Salmonella Typhimurium DT104, and Enterococcus faecium in peanut paste formulations at two different levels of water activity and fat. Journal of Food Protection, 77(8), 1252–1259. https://doi.org/10.4315/0362-028X.JFP-13-553
- Killalea, D., Ward, L. R., Roberts, D., Louvois, J., Sufi, F., Stuart, J. M., Wall, P. G., Susman, M., Schwieger, M., Sanderson, P. J., Fisher, I. S., Mead, P. S., Gill, O. N., & Rowe, B. (1996). International epidemiological and microbiological study of outbreak of *Salmonella* Agona infection from a ready to eat savoury snack–I: England and Wales and the United States. *British Medical Journal*, *313*, 7065, 1105–7. https://doi.org/10.1136/bmj.313.7065.1105
- Kim, J.-S., Liu, L., & Vázquez-Torres, A. (2021). The DnaK/DnaJ Chaperone System Enables RNA Polymerase-DksA Complex Formation in Salmonella Experiencing Oxidative Stress. American Society for Microbiology, 12(3), https://doi.org/10.1128/mBio. 03443-20
- Kim, J.-Y., Song, H., Kim, D., & Lee, S.-Y. (2021). Physiological changes and stress responses of heat shock treated Salmonella enterica serovar Typhimurium. Food Control, 124, 107915. https:// doi.org/10.1016/j.foodcont.2021.10791
- Kimber, M. A., Kaur, H., & Wang, L. (2012). Survival of Salmonella, Escherichia coli O157:H7, and Listeria monocytogenes on inoculated almonds and pistachios stored at –19, 4, and 24°C. Journal of Food Protection, 75(8), 1394–1403. https://doi.org/10.4315/0362-028X.JFP-12-023
- Kirk, M. D., Little, C. L., Lem, M., Fyfe, M., Genobile, D., Tan, A., Threlfall, J., Paccagnella, A., Lightfoot, D., Lyi, H., McIntyre, L., Ward, L., Brown, D. J., Susman, S., & Fisher, I. S. T (2004). An outbreak due to peanuts in their shell caused by *Salmonella enterica*

¹² WILEY Food Science

serotypes Stanley and Newport – Sharing molecular information to solve international outbreak. *Epidemiology and Infection*, *132*(4), 571–577. https://doi.org/10.1017/s095026880400216x

- Klingl, S., Kordes, S., Schmid, B., Gerlach, R. G., Hensel, M., & Muller, Y. A. (2021). Recombinant protein production and purification of SiiD, SiiE and SiiF - Components of the SPI4-encoded type I secretion system from *Salmonella* Typhimurium. *Protein Expression and Purification*, 172, 105632. https://doi.org/10.1016/j. pep.2020.105632
- Komitopoulou, E., & Peñaloza, W. (2009). Fate of Salmonella in dry confectionery raw materials. Journal of Applied Microbiology, 106, 1892–1900. https://doi.org/10.1111/j.1365-2672.2009.04144.x
- Kotzekidou, P. (1998). Microbial stability and fate of Salmonella Enteritidis in halva, a low-moisture confection. Journal of Food Protection, 61(2), 181–185. https://doi.org/10.4315/0362-028X-61.2.
 181
- Kurashova, N. A., Madaeva, I. M., & Kolesnikova, L. I. (2020). Expression of HSP70 Heat-Shock Proteins under Oxidative Stress. *Advances in Gerontology*, *10*(1), 20–25. https://doi.org/10.1134/ s2079057020010099
- Lamas, A., Miranda, J. M., Regal, P., Vázquez, B., Franco, C. M., & Cepeda, A. (2018). A comprehensive review of non-*enterica* subespecies of Salmonella enterica. *Microbiological Research*, 206, 60– 73. https://doi.org/10.1016/j.micres.2017.09.010
- Lehmacher, A., Bockemuhl, J., & Aleksic, S. (1995). Nationwide outbreak of human salmonelosis in Germany due to contaminated paprika and paprika-powdered potato chips. *Epidemiology and Infection*, 115(3), 501–511. https://doi.org/10.1017/ s0950268800058660
- Lian, F., Zhao, W., Yang, R., Tang, Y., & Katiyo, W. (2015). Survival of *Salmonella enteric* in skim milk powder with different water activity and water mobility. *Food Control*, 47, 1–6. https://doi.org/ 10.1016/j.foodcont.2014.06.03
- Liew, A. T. F., Foo, Y. H., Gao, Y., Zangoui, P., Singh, M. K., Gulvady, R., & Kenney, L. J. (2019). Single cell, super-resolution imaging reveals an acid pH-dependent conformational switch in SsrB regulates SPI-2. *Elife*, 8, e45311. https://doi.org/10.7554/eLife.45311
- Liu, S., Tang, J., Tadapaneni, R. K., Yang, R., & Zhu, M.-J. (2018). Exponentially Increased Thermal Resistance of Salmonella spp. and Enterococcus faecium at Reduced Water Activity. Applied and Environmental Microbiology, 84, e02742–17. https://doi.org/10. 1128/AEM.02742-17
- Liu, X., Fan, X., Wang, W., Yao, S., & Chen, H. (2021). Wetting raw almonds to enhance pulse light inactivation of *Salmonella* and preserve quality. *Food Control*, *125*, 107946. https://doi.org/10. 1016/j.foodcont.2021.107946
- Loh, E., Righetti, F., Eichner, H., Twittenhoff, C., & Narberhaus, F. (2018). RNA Thermometers in Bacterial Pathogens. *Microbiology Spectrum*, 6(2), https://doi.org/10.1128/microbiolspec.rwr-0012-2017
- Lou, L., Zhang, P., Piao, R., & Wang, Y. (2019). Salmonella Pathogenicity Island 1 (SPI-1) and Its Complex Regulatory Network. *Frontiers in Cellular and Infection Microbiology*, 9, 270. https://doi.org/10. 3389/fcimb.2019.00270
- Maduchanka, D. N. N., Jayaweera, T. S. P., Jayasinghe, J. M. C. S., Yasawathie, D. G., & Ruwandeepika, H. A. D. (2018). Decontaminating Effect of Organic Acids and Natural Compounds on Broiler Chicken Meat Contaminated with Salmonella Typhimurium.

Asian Food Science Journal, 3(1), 1–9. https://doi.org/10.9734/ AFSJ/2018/41802

- Mahendran, R., Ramanan, K. R., Barba, F. J., Lorenzo, J. M., López-Fernández, O., Munekata, E. S., Roohinejad, S., SantAna, A. S., & Tiwari, B. K. (2019). Recent advances in the application of pulsed light processing for improving food safety and increasing shelf life. *Trends in Food Science & Technology*, *88*, 67–79. https://doi.org/10. 1016/j.tifs.2019.03.010
- Mandal, R., Singh, A., & Singh, A. P. (2018). Recent developments in cold plasma decontamination technology in the food industry. *Trends in Food Science & Technology*, 80, 93–103. https://doi.org/ 10.1016/j.tifs.2018.07.014
- Maserati, A., Lourenco, A., Diez-Gonzalez, F., & Fink, R. C. (2018). iTRAQ-based Global Proteomic Analysis of *Salmonella enterica* serovar Typhimurium in Response to Desiccation, Low aw, and Thermal Treatment. *Applied and Environmental Microbiology*, *84*(18), E00393. https://doi.org/10.1128/aem.00393-18
- Mendonça, E. P., Melo, R. T., Oliveira, M. R. M., Monteiro, G. P., Peres, P. A. B. M., Fonseca, B. B., Giombelli, A., & Rossi, D. A. (2020). Characteristics of virulence, resistance and genetic diversity of strains of *Salmonella* Infantis isolated from broiler chicken in Brazil. *Brazilian Journal of Veterinary Research*, 40(1), 29–38. https://doi.org/10.1590/1678-5150-PVB-5546
- Merino, L., Procura, F., Trejo, F. M., & Bueno, D. J., & Golowczyc, M. A. (2017). Biofilm formation by *Salmonella* sp. in the poultry industry: Detection, control and eradication strategies. *Food Research International*, *119*, 530–540. https://doi.org/10.1016/j. foodres.2017.11.024
- Michael, M., Acuff, J. C., Vega, D., Sekhon, A. S., Channaiah, L. H., & Phebus, R. K. (2022). Survivability and thermal resistance of *Salmonella* and *Escherichia coli* O121 in wheat flour during extended storage of 360 days. *International Journal of Food Microbiology*, 362, 109495. https://doi.org/10.1016/j.ijfoodmicro. 2021.109495
- Ministry of Health (Brazil) (2011). Technical manual for laboratory diagnosis of Salmonella spp.: Laboratory diagnosis of the genus Salmonella. Ministry of Health.
- Ministry of Health (Brazil). (2019). Foodborne disease outbreaks in Brazil. https://antigo.saude.gov.br/images/pdf/2019/maio/17/ Apresentacao-Surtos-DTA-Maio-2019.pdf
- Ministry of Health (Brazil). (2020). Epidemiological bulletin. Outbreaks reported from waterborne diseases and food – Brazil, 2016–2019. https://www.gov.br/saude/pt-br/centraisde-conteudo/boletim-epidemiologico-svs-32-pdf/view
- Mutz, Y., da, S., Rosario, D. K. A., Paschoalin, V. M. F., & Conte-Junior, C. A. (2019). Salmonella enterica: A hidden risk for drycured meat consumption? *Critical Reviews in Food Science and Nutrition*, 1–15. https://doi.org/10.1080/10408398.2018.1555132
- Narayan, A., Campos, L. A., Bhatia, S., Fushman, D., & Naganathan, A. N. (2017). Graded Structural Polymorphism in a Bacterial Thermosensor Protein. *Journal of the American Chemical Society*, 139(2), 792–802. https://doi.org/10.1021/jacs.6b10608
- Nieto, P. A., Pardo-Roa, C., Salazar-Echegarai, F. J., Tobar, H. E., Coronado-Arrázola, I., Riedel, C. A., Kalergis, A. M., & Bueno, S. M. (2016). New insights about excisable pathogenicity islands in *Salmonella* and their contribution to virulence. *Microbes and Infection*, 18(5), 302–309. https://doi.org/10.1016/j.micinf.2016.02. 001

- Nummer, B. A., Shrestha, S., & Smith, J. V. (2012). Survival of Salmonella in a high sugar, low water-activity, peanut butter flavored candy fondant. Food Control, 27(1), 184–187. https://doi.org/ 10.1016/j.foodcont.2011.11.037
- Olaimat, A. N., Al-Nabulsi, A. A., Osaili, T. M., Al-Holy, M., Ayyash, M. M., Mehyar, G. F., Jaradat, Z., & Ghoush, M. A. (2017). Survival and inhibition of *Staphylococcus aureus* in commercial and hydrated tahini using acetic and citric acids. *Food Control*, 77, 179– 186. https://doi.org/10.1016/j.foodcont.2017.02.022
- Olaimat, A. N., Al-Holy Murad, A., Abu Ghoush, M., Al-Nabulsi, A. A., & Holley, R. A. (2018). Control of Salmonella enterica and Listeria monocytogenes in hummus using allyl isothiocyanate. International Journal of Food Microbiology, 278, 73–80. https://doi.org/ 10.1016/j.ijfoodmicro.2018.04.033
- Olaimat, A. N., Osaili, T. M., AL-Holy, M., Al-Nabulsi, A. A., Obaid, R. S., Alaboudi, A. R., Ayyash, M., & Holley, R. (2020). Microbial safety of oily, low water activity food products: A review. *Food Microbiology*, 92, 103571. https://doi.org/10.1016/j.fm.2020.103571
- Oner, M. E. (2017). Inactivation of Salmonella enteritidis on almonds by pulsed light treatment. Academic Food Journal/Akademik GIDA, 15(3), 242–248. https://doi.org/10.24323/akademik-gida. 345257
- Ozturk, S., Kong, F., & Singh, R. K. (2020). Evaluation of *Enterococcus faecium* NRRL B-2354 as a potential surrogate of *Salmonella* in packaged paprika, white pepper and cumin powder during radio frequency heating. *Food Control*, *108*, 106833. https://doi.org/10. 1016/J.FOODCONT.2019.106833
- Pi, X., Yang, Y., Sun, Y., Wang, X., Wan, Y., Fu, G., Xin, L., & Cheng, J. (2021). Food irradiation: a promising technology to produce hypoallergenic food with high quality. *Critical Reviews in Food Science and Nutrition*, 1–16. https://doi.org/10.1080/10408398.2021. 1904822
- Podolak, R., Enache, E., Stone, W., Black, D. G., & Elliott, P. (2010). Sources and risk factors for contamination, survival, persistence, and heat resistance of *Salmonella* in low-moisture foods. *Journal* of Food Protection, 73(10), 1919–1936. https://doi.org/10.4315/0362-028X-73.10.1919
- Podolak, R., & Black, D. G. (Eds.). (2017). Control of Salmonella and Other Bacterial Pathogens in Low Moisture Foods. Grocery Manufacturers Association, https://doi.org/10.1002/9781119071051
- Pradhan, D., & Devi Negi, V. (2019). Stress-induced adaptations in Salmonella: a ground for shaping its Pathogenesis. *Microbiological Research*, 229, 126311. https://doi.org/10.1016/j.micres.2019.126311
- Prasad, A., Ganzle, M., & Roopesh, M. (2019). Inactivation of *Escherichia coli* and *Salmonella* using 365 and 395 nm high intensity pulsed light emitting diodes. *Foods*, 8(12), 679. https://doi.org/ 10.3390/foods8120679
- Priya, G. B., Agrawal, R. K., Milton, A. A. P., Mishra, M., Mendiratta, S. K., Luke, A., & Rajkhowa, S. (2020). Rapid and visual detection of *Salmonella* in meat using invasion A (*invA*) gene-based loop-mediated isothermal amplification assay. *Food Science and Technology*, *126*(2020), 109262. https://doi.org/10.1016/j.lwt.2020. 109262
- Rayman, M. K., D'Aoust, J.-Y., Aris, B., Maishment, C., & Wasik, R. (1979). Survival of microorganisms in stored pasta. *Journal of Food Protection*, 42(4), 330–334. https://doi.org/10.4315/0362-028X-42.4. 330
- Reyes-Jurado, F., Navarro-Cruz, A. R., Méndez-Aguilar, J., Ochoa-Velasco, C. E., Mani-López, E., Jiménez-Munguía, M. T., Palou,

E., Lopez-Malo, A., & Ávila-Sosa, R. (2019). High-Intensity Light Pulses To Inactivate *Salmonella* Typhimurium on Mexican Chia (*Salvia hispanica* L.) Seeds. *Journal of Food Protection*, *82*(8), 1272–1277. https://doi.org/10.4315/0362-028x.jfp-18-5 77

Food Science WILEY 13

- Rolfe, C., & Daryaei, H. (2020). Intrinsic and Extrinsic Factors Affecting Microbial Growth in Food Systems. In: Demirci, A., Feng, H., Krishnamurthy, K. (eds) *Food Safety Engineering. Food Engineering Series*. Cham: Springer. https://doi.org/10.1007/978-3-030-42660-6_1
- Salive, A. F. V., Prudêncio, C. V., Baglinière, F., Oliveira, L. L., Ferreira, S. O., & Vanetti, M. C. D. (2020). Comparison of stress conditions to induce viable but non-cultivable state in Salmonella. *Brazilian Journal of Microbiology*, https://doi.org/10.1007/s42770-020-00261-w
- Scheil, W., Cameron, S., Dalton, C., Murray, C., & Wilson, D. (1998). A South Australian Salmonella Mbandaka outbreak investigation using a database to select controls. Australian and New Zealand Journal of Public Health, 22(5), 536–539. https://doi.org/10.1111/j. 1467-842x.1998.tb01434.x
- Serment-Moreno, V. (2020). Microbial Modeling Needs for the Nonthermal Processing of Foods. *Food Engineering Reviews*, 13, 465– 489. https://doi.org/10.1007/s12393-020-09263-8
- Sever, N. K., & Akan, M. (2019). Molecular analysis of virulence genes of SalmonellaInfantis isolated from chickens and turkeys. *Microbial Pathogenesis*, 126, 199–204. https://doi.org/10.1016/j.micpath. 2018.11.006
- Singh, Y., Saxena, A., Kumar, R., & Saxena, M. K. (2018). Virulence System of *Salmonella* with Special Reference to *Salmonella enterica*. In (Salmonella - A Re-Emerging Pathogen Ed.). *IntechOpen*. https://doi.org/10.5772/intechopen.77210
- Sirsat, S. A., Burkholder, K. M., Muthaiyan, A., Dowd, S. E., Bhunia, A. K., & Ricke, S. C. (2011). Effect of sublethal heat stress on *Salmonella* Typhimurium virulence. *Journal of Applied Microbiology*, *110*(3), 813–822. https://doi.org/10.1111/j.1365-2672.2011.04941.
- Stavropoulou, E., & Bezirtzoglou, E. (2019). Predictive Modeling of Microbial Behavior in Food. *Foods*, 8(12), 654. https://doi.org/10. 3390/foods8120654
- Steinbrunner, P. J., Limcharoenchat, P., Suehr, Q. J., Ryser, E. T., Marks, B. P., & Jeong, S. (2019). Effect of Food Structure, Water Activity, and Long-Term Storage on X-Ray Irradiation for Inactivating Salmonella Enteritidis PT30 in Low-Moisture Foods. Journal of Food Protection, 82(8), 1405–1411. https://doi.org/10.4315/ 0362-028X.JFP-19-091
- Sterniša, M., Sabotič, J., & Klančnika, A. (2022). A novel approach using growth curve analysis to distinguish between antimicrobial and anti-biofilm activities against Salmonella. *International Journal of Food Microbiology*, 364, 109520. https://doi.org/10.1016/ j.ijfoodmicro.2021.109520
- Subedi, S., Du, L., Prasad, A., Yadav, B., & Roopesh, M. S. (2020). Inactivation of Salmonella and Quality Changes in Wheat Flour after Pulsed Light-Emitting Diode (LED) Treatments. Food and Bioproducts Processing. S0960308519308855. https://doi.org/10.1016/ j.fbp.2020.02.004
- Sun, S., Anderson, N. M., & Keller, S. (2014). Atmospheric pressure plasma treatment of black peppercorns inoculated with *Salmonella* and held under controlled storage. *Journal of Food Science*, 79(12), E2441–E2446.

¹⁴ WILEY Food Science

- Syamaladevi, R. M., Tadapaneni, R. K., Xu, J., Villa-Rojas, R., Tang, J., Carter, B., Sablani, S., & Marks, B. (2016a). Water activity change at elevated temperatures and thermal resistance of *Salmonella* in all-purpose wheat flour and peanut butter. *Food Research International*, *81*, 163–170. https://doi.org/10.1016/j.foodres.2016.01.008
- Syamaladevi, R. M., Tang, J., Villa-Rojas, R., Sablani, S., Carter, B., & Campbell, G. (2016b). Influence of water activity on thermal resistance of microorganisms in low-moisture foods: a review. *Comprehensive Reviews In Food Science And Food Safety*, 15, 353–370. https://doi.org/10.1111/1541-4337.12190
- Tack, D. M., Marder, E. P., Griffin, P. M., Cieslak, P. R., Dunn, J., Hurd, S., Scallan, E., Lathrop, S., Muse, A., Ryan, P., Smith, K., Tobin-D'Angelo, M., Vuhia, D. J., Holt, K. G., Wolpert, B. J., Tauxe, R., & Geissler, A. L. (2019). Preliminary incidence and trends of infections with pathogens transmitted commonly through food — Foodborne diseases active surveillance network, 10 U.S. Sites, 2015–2018. Morbidity and Mortality Weekly Report, 68(16), 369–373. https://doi.org/10.15585/mmwr.mm6816a2
- Tadapaneni, R. K., Xu, J., Yang, R., & Tang, J. (2018). Improving design of thermal water activity cell to study thermal resistance of *Salmonella* in low-moisture foods. *LWT*, *92*, 371–379. https://doi. org/10.1016/j.lwt.2018.02.046
- Tamminga, S. K., Beumer, R. R., Kampelmacher, E. H., & Van Leusden, F. M. (1976). Survival of *Salmonella* Eastbourne and *Salmonella* Typhimurium in chocolate. *Journal of Hygiene*, 76(1), 41–47. https://doi.org/10.1017/s0022172400054929
- Tanner, J. R., & Kingsley, R. A. (2018). Evolution of Salmonella within hosts. Trends in Microbiology, https://doi.org/10.1016/j.tim.2018. 06.001
- Tapia, M. S., Alzamora, S. M., & Chirife, J. (2020). Effects of Water Activity (aw) on Microbial Stability as a Hurdle in Food Preservation. *Water Activity in Foods*, 323–355. https://doi.org/10.1002/ 9781118765982.ch14
- Tong, T., Wang, P., Shi, H., Li, F., & Jiao, Y. (2022). Radio frequency inactivation of E. coli O157: H7 and Salmonella Typhimurium ATCC 14028 in black pepper (piper nigrum) kernels: Thermal inactivation kinetic study and quality evaluation. *Food Control*, *132*, 108553. https://doi.org/10.1016/J.FOODCONT.2021.108553
- Uesugi, A. R., Danyluk, M. D., & Harris, L. J. (2006). Survival of Salmonella enteritidis phage type 30 788 on inoculated almonds stored at -20, 4, 23, and 35°C. Journal of Food Protection, 69(8), 1851-789 1857. https://doi.org/10.4315/0362-028x-69.8.1851
- Voss-Rech, D., Kramer, B., Silva, V. S., Rebelatto, R., Abreu, P. G., Coldbella, A., & Vaz, C. S. L. (2019). Longitudinal study reveals persistent environmental *Salmonella* Heidelberg in Brazilian broiler farms. *Veterinary Microbiology*, 233, 118–123. https://doi.org/10. 1016/j.vetmic.2019.04.004
- Wang, H., Ye, K., Cao, J., Xu, X.-L., Zhou, G. H., & Wei, X. (2013). Occurrence, antimicrobial resistance and biofilm formation of *Salmonella* isolates from a chicken slaughter plant in China. *Food Control*, 33, 378–384. https://doi.org/10.1016/j.foodcont.2013. 03.030

- Wason, S., Verma, T., & Subbiah, J. (2021). Validation of process technologies for enhancing the safety of low-moisture foods: A review. *Comprehensive Reviews in Food Science and Food Safety*, 20(5), 4950–4992. https://doi.org/10.1111/1541-4337.12800
- Werber, D., Dreesman, J., Feil, F., Van Treeck, U., Ethelberg, S., Hauri, A. M., Roggentin, P., Pragger, R., Fisher, I. ST., Behnke, S. C., Bartelt, E., Weise, E., Ellis, A., Siitonen, A., Anderson, Y., Tschape, H., Kramer, M. H., & Ammon, A. (2005). International outbreak of *Salmonella* Oranienburg due to German chocolate. *BMC Infectious Diseases*, 5(1), 7. https://doi.org/10.1186/1471-2334-5-7
- Xie, J., & Hung, Y. (2020). Efficacy of pulsed-ultraviolet light for inactivation of Salmonella spp on black peppercorns. Journal of Food Science, 85(3), 755–761. https://doi.org/10.1111/1750-3841.15059
- Xu, J., Tang, J., Jin, Y., Song, J., Yang, R., Sablnai, S. S., & Zhu, M.-J. (2019). High temperature water activity as a key factor influencing survival of *Salmonella* Enteritidis PT30 in thermal processing. *Food Control*, 520–528. https://doi.org/10.1016/j.foodcont.2018.11. 054
- Xu, J., Shah, D. H., Song, J., & Tang, J. (2020). Changes in cellular structure of heat-treated *Salmonella* in low-moisture environments. *Journal of Applied Microbiology*, 129(2), 434–442. https:// doi.org/10.1111/jam.14614
- Xu, C., Wang, F., Huang, F., Yang, M., He, D., & Deng, L. (2021). Targeting effect of berberine on type I fimbriae of Salmonella Typhimurium and its effective inhibition of biofilm. Applied Microbiology and Biotechnology, 105(4), 1563–1573. https://doi.org/ 10.1007/s00253-021-11116-1
- Xu, J., Xie, Y., Paul, N. C., Roopesh, M., Shah, D. H., & Tang, J. (2022). Water sorption characteristics of freeze-dried bacteria in low-moisture foods. *International Journal of Food Microbiology*, 362, 109494. https://doi.org/10.1016/j.ijfoodmicro.2021.109494
- Yang, X., Wu, Q., Zhang, J., Huang, J., Chen, L., Wu, S., Zeng, H., Wang, J., Chen, M., Wu, H., Qihui, G., & Wei, X. (2019). Prevalence, Bacterial Load, and Antimicrobial Resistance of *Salmonella* Serovars Isolated From Retail Meat and Meat Products in China. *Frontiers in Microbiology*, *10*, 2121. https://doi.org/10.3389/fmicb. 2019.02121
- Zhao, X., Zhao, F., Wang, J., & Zhong, N. (2017). Biofilm formation and control strategies of foodborne pathogens: food safety perspectives. *Royal Society of Chemistry Advances*, 7, 36670–36683. https: //doi.org/10.1039/C7RA02497E

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