Review article

Psychrotrophic Bacteria Threatening the Safety of Animal-derived Foods: Characteristics, Contamination, and Control Strategies

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Abstract

Animal-derived foods, such as meat and dairy products, are prone to spoilage by psychrotrophic bacteria due to their high-water activity and nutritional value. These bacteria can grow at refrigerated temperatures, posing significant concerns for food safety and quality. Psychrotrophic bacteria, including *Pseudomonas*, *Listeria*, and *Yersinia*, not only spoil food but can also produce heat-resistant enzymes and toxins, posing health risks. This review examines the characteristics and species composition of psychrotrophic bacteria in animal-derived foods, their impact on food spoilage and safety, and contamination patterns in various products. It explores several nonthermal techniques to combat bacterial contamination as alternatives to conventional thermal methods, which can affect food quality. This review highlights the importance of developing nonthermal technologies to control psychrotrophic bacteria that threaten the cold storage of animal-derived foods. By adopting these technologies, the food industry can better ensure the safety and quality of animal-derived foods for consumers.

Keywords: Animal-derived foods, Psychrotrophic bacteria, Prevalence, Nonthermal techniques, Food safety

Introduction

Animal-derived foods, such as meat, milk, and their processed products, generally have high water activity and nutritional value. Therefore, they are highly susceptible to spoilage by microorganisms, especially pathogenic bacteria (Odeyemi et al., 2020; Saha et al., 2024; Tapia et al., 2020; Yuan et al., 2019). A cold chain system is the simplest way to control the freshness and microbiological safety of animal-derived foods. By applying this system, food quality is maintained by controlling the temperature at a low level during the entire process of harvesting fresh foods from the production site and then storing and transporting them to the final consumption site (Montanari, 2008; Ndraha et al., 2018). However, this approach is not perfect, as some microorganisms survive and multiply even at low temperatures. Low-temperature storage improves food storability; however, contamination with psychrotrophic bacteria may make this impossible (Chen et al., 2020).

Psychrotrophic bacteria, defined as cold-tolerant bacteria, have the ability to grow at temperatures below 7°C, such as those found in refrigerated conditions. These bacteria are known for causing spoilage in food products, especially animal-derived foods (Moyer et al., 2017; Tatini and Kouppi, 2002). Psychrotrophic bacteria can grow at low temperatures, although their growth is limited to a maximum temperature of approximately 20°C. Typically, these bacteria do not thrive over 35°C (Kanekar and Kanekar, 2022). Thus, they appear to be a subgroup of mesophiles, whose optimum growth range is between 30°C to 40°C. However, they are not a subgroup of psychrophiles, which prefer much colder environments, typically below 15°C (Cavicchioli, 2016). During storage at low temperatures, psychrotrophic bacteria that adapt to the low temperatures thrive better than mesophilic bacteria, leading to an increase in their cell population (Samaržija et al., 2012; Wickramasinghe et al., 2019). Moreover, compared to the mesophilic bacteria in raw milk, the quantity of psychrotrophic bacteria

increased by over 10%. Psychrotrophic bacteria can produce enzymes related to heat resistance (e.g., proteolytic enzymes, lipolytic enzymes, and phospholipases), some of which have antibiotic resistance or the ability to produce toxins. Thus, psychrotrophic bacteria proliferate at low temperatures and not only spoil food but can also be difficult to inactivate through heat treatment (sterilization process) and can have adverse effects on human health.

Therefore, in this review, we aimed to determine the growth characteristics and species composition of psychrotrophic bacteria that are commonly observed in animal-derived foods and to check their contamination (distribution) status. In addition, we proposed a technique for reducing the number of psychrotrophic bacteria that can be applied to animal-derived food.

Characteristics of psychrotrophic bacteria

Psychrotrophic bacteria enter food from their mesophilic habitats and continue to grow at a slow pace in refrigerated environments. There are several reasons why psychrotrophic bacteria can continue to survive and grow even at low temperatures. First, they can maintain the activity of various enzymes involved in metabolism even under cold conditions. These bacteria possess enzymes that can be activated at low temperatures, and they provide thermolability and increase complementarity between the substrate and the active site, thereby providing high specific activity at low temperatures (Cavicchioli et al., 2002; Chattopadhyay, 2006; d'Amico et al., 2002). As a result, the activation energy is lowered, helping to maintain the substrate-enzyme reaction even at low temperatures (De Maayer et al., 2014). Second, they can maintain the membrane fluidity even at low temperatures due to their ability to regulate the composition of the cell membranes. The cell membrane transmits various signals and exchanges substances, especially nutrients. Therefore, cellular survival is highly dependent on the fluidity of the cell membrane (Moyer et al., 2017; Najjar et al., 2007; Wang et al., 2016). The membrane fluidity

is determined by composition of the phospholipid bilayer comprising the cell membrane, which is odd-numbered, unsaturated, and anteiso fatty acids (Hagve, 1988; Yoon et al., 2015). Especially, polyunsaturated fatty acids (PUFAs) had a low melting point, thus controlling the amount of PUFAs at low temperatures can be a good way to maintain membrane fluidity (Casanueva et al., 2010; Hassan et al., 2020a). Moreover, a-$C_{15:0}$, an anteiso fatty acid, plays a key role in bacterial survival at low temperatures; for example, a-$C_{15:0}$ is a major component of bacteria living in the Antarctic region (Chattopadhyay and Jagannadham, 2003). In addition to changes in the composition of fatty acids in the cell membrane, changes in various transport proteins, which play a role in transporting substances into and out of the cytoplasm, also occur in the cell membrane. Psychrotrophic bacteria upregulate the expression of some of these proteins to ensure smooth transport of substances even at low temperatures (De Maayer et al., 2014). Third, they have or can uptake some substances that help them survive at low temperatures, such as antifreeze proteins (AFPs) and compatible solutes. AFPs, possess by psychrotrophic bacteria, which control the expression of proteins related to cold and heat shock, or by switching to a viable but nonculturable state (Chattopadhyay, 2006). They can prevent freezing or thawing damage to bacteria by inhibiting the growth of ice crystals at low temperatures (Celik et al., 2013). Psychrotrophic bacteria can respond to low temperatures by accumulating compatible solutes in the cytoplasm to increase the concentration of solutes and thereby increasing osmotic pressure (Casanueva et al., 2010). For example, glycine betaine, a type of compatible solute, is a substance that *L. monocytogenes* can synthesize, and its synthesis becomes active at low temperatures, which can stimulate the growth of *L. monocytogenes* at low temperatures (Beumer et al., 1994; Zeisel et al., 2003; Chan and Wiedmann, 2008). It should be remembered that all of the previously mentioned events are regulated by gene expression.

Psychrotrophic bacteria are the main cause of the spoilage of chilled and frozen foods derived from animals, including raw or cooked meat, dairy products, butter, fresh or cooked seafood, and vegetables (Wei et al., 2019). The most common psychrotrophic bacteria found in animal-derived food are *Pseudomonas*, *Listeria*, *Yersinia*, *Serratia*, *Aerococcus*, *Acinetobacter*, and *Flavobacterium* (Chen et al., 2020; Ribeiro Júnior et al., 2018; Yuan et al., 2017). *Pseudomonas* is the main bacterium that causes meat spoilage because it produces protein and fat hydrolases, biosurfactants, and colors (Rouger et al., 2018). Dhama et al. (2013) reported that meat and meat products, and dairy products are common sources of *Listeria monocytogenes*, an intracellular gram-positive bacterium that may survive and grow under refrigeration.

Contamination of animal-derived food due to psychrotrophic bacteria

Animal-derived foods often contaminated by psychrotrophic bacteria, including *Listeria*, *Pseudomonas*, and *Yersinia*. Numerous studies have reported cases of contamination in a variety of animal resources, including dairy products (milk and cheese), meat (poultry, pork, and beef), and animal-derived products (Table 1). Despite not being classified as a psychrotrophic bacterium, *Clostridium* has been commonly detected in animal-derived foods stored at low temperature.

Listeria monocytogenes

Listeria spp. have been identified in various animal-derived food sources across different regions, highlighting their prevalence in the food chain and their potential risks to public health. Particularly concerning for animal-derived food safety is the fact that *L. monocytogenes* can grow at refrigerated conditions. Raw milk and cheese (Akrami-Mohajeri et al., 2018; Costanzo et al., 2020; Rahimi et al., 2010), meats (Li et al., 2018; Oswaldi et al., 2021), and ready-to-eat (RTE) meat products (Calvo-Arrieta et al., 2021; Meza-Bone et al., 2023) are the most common

128 animal-derived foods contaminated with *L. monocytogenes*. In Syria, research has shown that
129 11.0% of raw milk samples tested positive for *Listeria* spp. (Al-Mariri et al., 2013). In Egypt,
130 *Listeria* spp. were found in cheese and raw milk at rates ranging from 3.3 to 6.6% (Ismaiel et
131 al., 2014). In Turkey, Kahraman et al. (2010) found that 4.8% of *L. monocytogenes* was detected
132 in white cheese samples, whereas processed cheese samples had a detection rate of 1.4%. In
133 Mexico, *L. monocytogenes* was detected in 9.3% of queso fresco, 12% of adobera, and 6% of
134 panela cheese, all of which are type of fresh cheese (Beltran et al., 2015; Torres-Vitela et al.,
135 2012). In South Africa, *L. monocytogenes* was detected in a range of meat and meat products
136 obtained from cattle, pork, sheep, game meat, and poultry (Matle et al., 2019). In this study, *L.*
137 *monocytogenes* were found in 10.1% of uncooked whole meat, 13.5% of RTE meat products,
138 and 19.5% of uncooked processed meat. In Spain, Vitas and Garcia-Jalon (2004) analyzed 396
139 meat product samples obtained from 55 small meat-processing plants, and *L. monocytogenes*
140 were detected in 36.1% of poultry meat, 34.9% of minced pork and beef. In Quevedo, a city in
141 Ecuador, 16.3% of *L. monocytogenes* was present in RTE meat products, including grilled
142 hamburger meat, mortadella, and salami. The concentration of *L. monocytogenes* ranged from
143 4 to 6 Log CFU/g, or possibly much higher (Meza-Bone et al., 2023).

144 ***Pseudomonas* spp.**

145 *Pseudomonas* is a prevalent member of the microbiota in various animal-derived foods,
146 including pork (Bruckner et al., 2012), chicken (Elbehiry et al., 2022; Wu et al., 2023), beef
147 (Ercolini et al., 2009), and milk (Yang et al., 2020). Wu et al. (2023) identified 109 *P.*
148 *aeruginosa* isolates, which constituted 42.1% of 259 samples collected across six districts in
149 Beijing, China. Especially, 91 isolates from chicken samples (54.2%) and 18 from pork samples
150 (19.8%). Similarly, Mahato et al. (2020) described that *P. aeruginosa* was detected in 46.7% of
151 chicken meat samples. Among the 370 meat and meat product samples analyzed by Rezaloo et

al. (2022), 29 samples were contaminated with *P. aeruginosa*. Notably, imported frozen beef harbored the highest prevalence (20%), followed by frozen beef (13.33%) and fresh beef samples (5.0%). Benie et al. (2017) reported that the prevalence of *P. aeruginosa* among smoked fish, fresh fish, and beef samples was 23.57%, 37.69%, and 53.04%, respectively. Furthermore, *P. aeruginosa* prevalence among sausage, luncheon meat, beef burger, and frozen burger samples was 8.33%, 18.3%, 1.67%, and 4.0%, respectively (Hassan et al., 2020b; Sofy et al., 2017). In the dairy foods, *P. aeruginosa* was detected in 70.0% of milk samples and 24.0% of samples collected from a milk tank at a dairy cattle farm in Egypt (Aziz et al., 2022). Additionally, Yang et al. (2020) isolated 153 *Pseudomonas* colonies from 20 raw milk samples in China and classified 31 strains as *P. fluorescens* and 18 as *P. lurida*. Carminati et al. (2019) found that *Pseudomonas* spp. was isolated from 50.0% of milk and 15.0% of cheese samples, with concentrations between 3.45 and 4.05 Log CFU/mL or g. Similarly, Arslan et al. (2011) reported that 22.9% of *Pseudomonas* spp. was isolated from 140 homemade white cheese samples, with the dominant isolate being *P. pseudoalcaligenes* (15.0%), followed by *P. alcaligenes* (5%), *P. aeruginosa* (1.4%), and *P. fluorescens* biovar V (0.7%). Furthermore, certain *Pseudomonas* species, including potentially pathogenic ones like *P. fulva*, *P. aeruginosa,* and *P. putida* have been found in the fecal samples of healthy animals. A study analyzing 704 animal fecal samples identified 133 isolates of *Pseudomonas* spp. belonging to 23 different species, recovered from 46 samples (6.5%) (Ruiz-Roldan et al., 2020).

Yersinia enterocolitica

Yersinia, particularly *Y. enterocolitica*, has been isolated and found to contaminate various types of animal-derived foods, such as raw and undercooked pork meats, milk, and dairy products (Ali et al., 2021). *Yersinia* presence in animal-derived foods poses significant public health risks as it can cause yersiniosis, which can range from mild self-limiting gastroenteritis

to more severe illnesses, including septicemia and yersinia enterocolitis (Hordofa, 2021). Swine serves as the main reservoir for *Y. enterocolitica*, with pathogenic strains found in swine and pork products are most commonly reported in human illnesses (MacDonald et al., 2012). Further food-producing animals that have been linked to *Y. enterocolitica* include sheep, poultry, and cattle. Palau et al. (2024) isolated *Y. enterocolitica* from 53 (75.7%) of 70 samples, including 37 from 50 chicken (74%), 8 from 10 pork (80%), and 8 from 10 salmon (80%). Similarly, Davies et al. (2001) found *Y. enterocolitica* in 80% of European salmon products. In France, *Y. enterocolitica* was found in 5.9% of chicken and 5.2% of pork samples (Esnault et al., 2013). Furthermore, Soltan Dallal et al. (2010) recovered *Yersinia* spp. from 16% of 379 samples, with 21.6% from chicken and 10% from beef. The detection rates of *Y. enterocolitica* in chicken and beef were 16% and 9.5%, respectively. In the dairy foods, *Y. enterocolitica* was detected in 12.2% of dairy products made from raw milk, 27.3% of raw cow milk, and 25% of raw goat milk collected from Apulia and Basilicata regions in Southern Italy (Mancini et al., 2022). Ahmed et al. (2019) reported that *Y. enterocolitica* was isolated from raw milk and dairy products in 10% of examined samples. Notably, the highest isolation rate was 22% from raw milk, followed by 12%, 4%, and 2% from fermented milk, pasteurized milk, and ripened salted cheese, respectively. Additionally, in Iran, *Y. enterocolitica* was isolated from 4.3% of bulk raw milk samples including cow, sheep, and goat milk (Jamali et al., 2015).

***Clostridium* spp.**

Clostridium spp. is generally not considered psychrotrophic bacteria, however, it is notable for their ability to produce endospores that can endure diverse environmental conditions, including cold temperatures. *Clostridium botulinum* and *Clostridium perfringens* are recognized for their potential to induce foodborne illnesses through toxins or spores (Grenda et al., 2017). Additionally, *C. botulinum* can be found in honey as dormant spores. The low water activity

and pH (acidic) of honey, which generally inhibit the growth of many bacteria, did not affect *C. botulinum* spores. Grenda et al. (2018) reported a 2.1% prevalence of *C. botulinum* in honey samples in Poland. Additionally, Maikanov et al. (2019) found that *C. botulinum* was isolated in only 0.5% of the samples, and *C. perfringens* was isolated from 18 (9%) of the 197 honey samples. One incidence of newborn botulism was reported in the United Kingdom in 2001, and it seemed that the cause was powdered infant formula contaminated with *C. botulinum* spores (Brett et al., 2005). According to Barash et al. (2010), 78% of the powdered infant formula samples contained clostridial spores, specifically *C. sporogenes*. The isolation of clostridial spores indicates that neurotoxic clostridial spores may be found in these products. In Italy, clostridial spores were detected in 99% of the 527 analyzed sheep milk samples. Among these samples, 86% had spore concentrations higher than the 1,000 spores/L (Turchi et al., 2016). Furthermore, *C. perfringens* was found in 98.7% of raw milk in tanks and 100% of curd samples used for Grana Padano cheese production in Northern Italy (Feligini et al., 2014). In meat and meat products, *C. perfringens* was detected in 50% of beef, 22.5% of lamb, 27.5% of ground beef, and 40% of minced lamb by Issimov et al. (2022). Shaltout et al. (2017) reported that *C. perfringens* was detected in 15.0% of beef and chicken before and after cooking, represented by 24% of raw chicken, 12% of cooked chicken, 16% of raw beef, and 8% of cooked beef samples.

Reduction of psychrotrophic bacteria in animal-derived foods

Thermal technologies have been used to deactivate microorganisms present in animal-derived food products. However, these techniques have a negative effect on the nutritional and sensory values of the treated food products (Jauhar et al., 2020). Conventional decontamination technologies for meat and meat products include heat processing, chilled storage, vacuum

224 packing, and chemical preservation. However, the use of heat during processing might reduce
225 the nutritional value and sensory characteristics, while chemically treated products might show
226 significant residue deposition (Jadhav et al., 2021). To eliminate pathogenic bacteria from
227 animal-derived foods without heating and affecting the quality of the food, nonthermal
228 techniques have been presented as alternatives to conventional pasteurization (Lee and Yoon,
229 2024). The various specific nonthermal techniques are described below.

230 ***Use of gas***

231 Each microorganism has its own unique oxygen requirement, and therefore, the growth of
232 microorganisms can be controlled by changing the air composition. One method of adjusting
233 the composition of air is the modified atmosphere packaging (MAP). This method particularly
234 focuses on aerobic microorganisms because it replaces oxygen in the air with carbon dioxide
235 or nitrogen (Farber et al., 2003; Kader, 1986). It not only inhibits the growth of aerobic
236 microorganisms, but also prevents rancidity of fat caused by oxygen, thus it can be effectively
237 applied to meat products containing fat. As an example, *Y. enterocolitica* and *L. monocytogenes*
238 might survive in MAP foods between 0 to 1°C (Barakat and Harris, 1999; Hudson et al., 1994).
239 When pure nitrogen gas was injected into raw milk, the *Pseudomonas* growth was significantly
240 limited, and when carbon dioxide was added to raw milk, the microbiological quality was
241 maintained for a long period of time, making it possible to produce milk with a long shelf life
242 (Munsch-Alatossava et al., 2010; Vianna et al., 2012; Yuan et al., 2019). In contrast, Huang et
243 al. (2020) reported higher concentrations of *Pseudomonas* in roasted chicken stored under
244 MAP (40% CO_2/60% N_2) conditions. Also, it has limitations in that spoilage caused by lactic
245 acid bacteria (LAB) is occasionally observed. LAB lowers pH and causes muscle tissue
246 destruction and moisture lose in meat stored under high CO_2 level (Wang et al., 2017;
247 Wickramasinghe et al., 2019).

Additionally, supercritical carbon dioxide (SC-CO_2) can be used to control pathogenic bacteria in animal-derived foods. SC-CO_2 diffuses CO_2 to lower cytoplasmic pH and extracts important components to change microbial cell membranes (Guerrero et al., 2017). It is currently not known how SC-CO_2 exhibits bactericidal activity, potentially, might depend on variables including pressure, temperature, and exposure time. According to the previous studies, SC-CO_2 might enhance membrane fluidity and permeability, as well as its ability to extract membrane components such as phospholipids (Budisa et al., 2014; Jauhar et al., 2020). Wei et al. (1991) initially investigated the inactivation of *L. monocytogenes* and *Salmonella* in spiked chicken meat using SC-CO_2 treatment, and 1-2 Log CFU/g of *L. monocytogenes* and *Salmonella* were reduced at 13.7 MPa and 35°C for 2 h. Furthermore, Ferrentino et al. (2013) reported that the growth of *L. monocytogenes* in dry-cured ham was reduced by 3 Log CFU/g at 45°C and 12 MPa for 5 min, and by 7 Log CFU/g at 50°C and 12 MPa for 15 min.

The application of cold plasma treatment has generated significant attention as a low-energy, non-thermal, and eco-friendly technique (Koddy et al., 2021). Previous studies have shown that the application of cold plasma can extend the storage duration of food products by inactivating bacteria and enzymes, while maintaining the overall quality of the food (Koddy et al., 2021; Zhang et al., 2021). The cell membrane and enzymes are predominantly damaged by reactive nitrogen species (RNS) and reactive oxygen species (ROS) during cold plasma treatment (Kang et al., 2021; Liao et al., 2017). Kim et al. (2011) reported a decrease of about 1–2 Log CFU/g for *L. monocytogenes*, *Esherichia coli*, and *Salmonella* on sliced bacon when treated with He and He/O_2 plasmas. Ulbin-Figlewicz et al. (2014) found a notable reduction of 2 Log CFU/g for *Y. enterocolitica* within 2 min and 2 Log CFU/g for *P. fluorescens* after 5 and 10 min of exposure to cold plasma for beef.

Lytic bacteriophages

Bacteriophage (Phage) refers to a virus that uses bacteria as a host, and when infected with a specific bacterium, it has a life cycle of self-proliferating within the bacterium and lysis the bacterium (Cooper, 2016). Phages are increasingly being applied as a biological control method to improve the microbiological safety in the food industry. Currently, phages targeting bacteria such as *L. monocytogenes* are being sold with approval from the Food and Drug Administration (Moye et al., 2018). LISTEX P100 phage is one of the phages that fight against *L. monocytogenes*, and effectively reduced *L. monocytogenes* (2.5 Log units reduction) that had been artificially contaminated in Brazilian fresh sausages (Rossi et al., 2011). Commercial phages based on LISTEX P100 are safe enough to be registered as GRAS (Sillankorva et al., 2012). Mohammadi et al. (2022) examined phages effect of *C. perfringens* lysis, and phages induced survival of *C. perfringens* in pasteurized milk and chicken meat. The effect of phages to lyse bacteria becomes stronger when bacteria are metabolically active, so the effect is better at room temperature or 37°C rather than at low temperatures (Cooper, 2016; Tomat et al., 2018). Since decreased metabolism of bacteria means decreased metabolism of phages, the latency period of phages may be somewhat longer at low temperatures. Nevertheless, since the bacterial lytic ability of phages is clearly observed even at low temperatures (Cooper, 2016), it may be effective in controlling the growth of psychrotrophic bacteria.

High pressure processing (HPP)

High-pressure processing (HPP) is a non-thermal technique that changes protein structure, causes protein denaturation, and lowers enzyme activity in microorganisms in order to prevent the growth of pathogenic psychrotrophic bacteria (Hurtado et al., 2019; Wisniewski et al., 2024). HPP increases the duration that various foods, including seafood, dairy products, meat products (RTE sliced deli meat, dry-cured meat, and hotdog products), and liquid products (fruit juices and purees), may be stored without spoiling. The storage duration of products

preserved with this technology is a few days to a few weeks, and they should be kept at a temperature below 7°C (Silva et al., 2023). Park et al. (2022) reported a significant reduction in *L. monocytogenes* in raw beef when treated with HPP for 2 to 7 min at 500 MPa and 4°C, decreasing from 3.9 to 6.5 Log CFU/g. In contrast, Stratakos et al. (2019) reported that extending the duration of HPP treatment from 3 to 5 min at pressure of 400, 500, and 600 MPa at 18°C in raw milk only slightly increased *L. monocytogenes* decline from 5.7 to 5.9 Log CFU/g. However, HPP has several limitations, including difficulties in commercialization due to high installation and maintenance costs (Aganovic et al., 2017). Furthermore, HPP is ineffective against spores and certain enzymes that are resistant to pressure, and it may induce color changes in some animal foods (Bolumar et al., 2020; Myers et al., 2013).

Ohmic heating

Ohmic heating is an innovative technique for heating food substances promptly, uniformly, and efficiently and is effective at inactivating microorganisms (Richa et al., 2017). The importance of the relationship between metallic prosthetic groups (polyphenol oxidase, lipoxygenases, and alkaline phosphatase) and electric current was emphasized by Makroo et al. (2020). Ohmic heating, depending on variables such as electrical conductivity, time, and electric field strength, effectively eliminates pathogens (*L. monocytogenes*, *E. coli*, and *Salmonella*) and spoilers (*Leuconostoc mesenteroides* and *P. aeruginosa*) in animal-derived foods (Lee et al., 2012; Saxena et al., 2016). *Salmonella* in baby formula and *Streptococcus thermophilus* in milk were reduced by about 5 Log CFU/mL at 60ºC in 2.91 min and 15 min, respectively, using ohmic heating, which demonstrated a more intense inactivation rate than conventional heating (Pires et al., 2021; Sun et al., 2008). Furthermore, ohmic heating reduced *P. aeruginosa* in meatball samples by 3 Log CFU/g at 125°C for 5 min (Mitelut et al., 2011).

Ultraviolet light

Ultraviolet (UV) light, with wavelengths ranging from 100 to 400 nm (Barba et al., 2017), has been used to increase the storage duration of various animal-derived foods by bactericidal inactivation and enzyme inhibition (Manzocco et al., 2009; Monteiro et al., 2020; Visuthiwan and Assatarakul, 2021). UV light can deactivate microbial enzymes through: (1) UV radiation is absorbed by chromophore groups or proteins, which produces excited states or radicals, and (2) proteins can be indirectly oxidized by singlet oxygen, which is formed from other chemicals that absorb light energy. These actions can cause oxidative stress, leading to alterations in the three-dimensional conformation of proteins and a decrease in their catalytic activity (Lante et al., 2013). UV-C light decreased the counts of *L. monocytogenes*, *Pseudomonas* spp., and β-lactamase producing bacteria from 1.1 to 2.8 Log CFU/cm^2 at 0.05 to 3 J/cm^2 (10 mW/cm^2, from 5 to 300 s) (Mcleod et al., 2018). Additionally, *Brochothrix thermosphacta* and *Y. enterocolitica* counts were decreased by up to 1.1 Log CFU/g and 0.8 Log CFU/g, respectively, by UV-C light during refrigerated storage at concentrations of 408 and 4,080 mJ/cm^2 (Reichel et al., 2020).

Conclusion

Psychrotrophic bacteria present a significant challenge in maintaining the safety and quality of animal-derived foods during storage and transportation, particularly under refrigerated conditions. Understanding the characteristics and prevalence of these bacteria as well as their contamination patterns in various animal resources is crucial for implementing effective control measures. Nonthermal techniques offer promising alternatives to traditional thermal techniques for reducing psychrotrophic bacterial contamination in animal-derived foods while preserving their sensory and nutritional properties. Further research and implementation of these technologies are essential to ensure the microbiological safety and storage duration of animal-

derived products in the food industry.

Conflict of Interest

The authors declare no potential conflict of interest.

Ethics Approval

This article does not require IRB/IACUC approval because there are no human and animal participants.

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718

719 **Table 1. Summary of the studies reporting the prevalence of psychrotrophic bacteria in**
720 **animal-derived foods**

Microorganisms	Type of foods		No. of positive samples (%)	Reference
Listeria spp.	Dairy products	Raw sheep milk	14/62 (11.1)	Rahimi et al., 2010
		Raw cow milk	10/90 (22.6)	
		Raw goat milk	4/60 (6.7)	
		Cheese	17/90 (18.9)	
		Ice cream	7/68 (10.3)	
		Butter	2/40 (5.0)	
		Raw milk	41/140 (29.2)	Akrami-Mohajeri et al., 2018
		Cheese	17/120 (14.1)	
		Butter	4/100 (4.0)	
		Raw milk	2/30 (6.6)	Ismaiel et al., 2014
		Raw milk	84/766 (11.0)	Al-Mariri et al., 2013
Listeria monocytogenes	Meat	Pig carcass	12/430 (2.8%)	Oswaldi et al., 2021
		Raw pork	104/356 (29.2)	Li et al., 2018
		Raw meat	98/525 (18.7)	Kramarenko et al., 2013
		Frozen lean beef	1/30 (3.3)	Ismaiel et al., 2014
		Raw meats (minced pork and beef meat)	103/295 (34.9)	Vitas and Garcia-Jalon (2004)
		Poultry	57/158 (36.1)	
		Raw processed meat	149/765 (19.5)	Matle et al. (2019)
		Raw intact meat	56/557 (10.1)	

	Dairy products	White cheese	5/105 (4.8)	Kahraman et al., 2010
		Processed cheese	1/70 (1.4)	
		Queso fresco cheese	7/75 (9.3)	Beltran et al., 2015
		Adobera cheese	12/100 (12)	Torres-Vitela et al., 2012
		Panela cheese	6/100 (6)	
	RTE meat products	Ham and turkey	6/507 (1.2)	Lambertz et al., 2012
		RTE milk products	13/4901 (0.3)	Kramarenko et al., 2013
		RTE meat products	135/6746 (2.0)	
		RTE meat products	59/436 (13.5)	Matle et al. (2019)
Pseudomonas spp.	Dairy products	Raw milk	93/103 (90.3)	Marchand et al., 2012
		Raw milk	18/20 (90.0)	Yang et al., 2020
		Raw milk	35/50 (70.0)	Aziz et al., 2022
		Milk (raw, n=4; pasteurized, n=8)	6/12 (50.0)	Carminati et al., 2019
		Cheese	3/20 (15.0)	
		White cheese	32/140 (22.9)	Alslan et al., 2011
	Meat	Chicken meat	7/15 (46.7)	Mahato et al., 2020
		Chicken meat	91/168 (54.2)	Wu et al., 2023
		Pork meat	18/91 (19.8)	

		Frozen chicken meat	69/320 (21.6)	Elbehiry et al., 2022
		Fresh beef	3/60 (5.0)	Rezaloo et al., 2022
		Frozen beef	8/60 (13.33)	
		Beef	122/230 (53.04)	Benie et al., 2017
		Smoked fish	33/140 (23.57)	
		Fresh fish	49/140 (37.69)	
	RTE meat product	Sausage	5/60 (8.33)	Sofy et al., 2017
		Luncheon meat	11/60 (18.3)	
		Beef burger	1/60 (1.67)	
		Frozen burger	1/25 (4.0)	Hassan et al., 2020
	Animal	Fecal samples	46/704 (6.5)	Ruiz-Roldan et al., 2020
Yersinia enterocolitica	Dairy products	Dairy products (cheese, butter, and yogurt)	6/49 (12.2)	Mancini et al., 2022
		Raw cow milk	12/44 (27.3)	
		Raw goat milk	1/4 (25.0)	
		Raw milk	19/446 (4.3)	Jamali et al., 2015
		Raw milk	11/50 (22.0)	Ahmed et al., 2019
		Fermented milk	6/50 (12.0)	
		Pasteurized milk	2/50 (4.0)	
		Ripened salted cheese	1/50 (2.0)	
	Meat	Chicken	132/720 (18.3)	Momtaz et al., 2013
		Chicken	37/50 (74)	Palau et al., 2024
		Pork	8/10 (80)	
		Salmon	8/10 (80)	

		Salmon	4/5 (80)	Davies et al., 2001
		Pork	11/237 (5.2)	Esnault et al., 2013
		Beef	11/210 (5.2)	
		Poultry	12/202 (5.9)	
		Chicken	41/190 (16)	Soltan Dallal et al. (2010)
		Beef	19/189 (9.5)	
Clostridium botulinum	Honey	Polish honey	5/240 (2.1)	Grenda et al, 2018
		Kazakh honey	1/197 (0.5)	Maikanov et al., 2019
Clostridium perfringens			18/197 (9.1)	
	Dairy products	Raw milk	78/79 (98.7)	Feligini et al., 2014
		Curd	79/79 (100)	
	Meat and meat products	Beef	20/40 (50)	Issimov et al., 2022
		Lamb	9/40 (22.5)	
		Ground beef	11/40 (27.5)	
		Minced lamb	16/40 (27.9)	
		Raw chicken	6/25 (24.0)	Shaltout et al., 2017
		Raw beef	4/25 (16.0)	

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