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LACTIC ACID BACTERIA: TWO SIDES OF THE SAME COIN

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Abstract
This review systematizes current data on the dual role of LABs. On the one hand, they are the basis for biopreservation as a source of bacteriocins and organic acids and serve as probiotics in fermented products. On the other hand, psychrotrophic strains of Lactobacillus, Leuconostoc, Carnobacterium, and Weissella are adapted to refrigerated storage and modified atmosphere packaging conditions, making them key spoilage agents in meat products, causing acidification, gas production, and slime formation. A particular problem is their ability to form resistant biofilms on processing equipment, leading to cross-contamination. The paper substantiates the need to move from generalized approaches to precise, strain-specific control. An effective risk management strategy should integrate modern methods of molecular monitoring (metagenomics, MALDI-TOF MS) to trace contamination sources; the development of targeted sanitation procedures against biofilms; and the implementation of biological control methods using antagonist cultures. It is concluded that the future of sustainable LAB use lies in an integrated approach that maximizes their beneficial potential for biopreservation and food fortification while simultaneously employing advanced scientific methods to mitigate the associated spoilage risks.

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Introduction

The growing consumer demand for "clean label" products (free from chemical preservatives) brings the modern food industry to a fundamental dilemma regarding lactic acid bacteria (LABs). The reduction in the use of traditional preservatives in the production of natural deli meat products, prepared salads, and fermented foods increases the vulnerability of products to microbiological spoilage, which often occurs without obvious external signs [1]. Furthermore, LABs are becoming the key agents determining both the safety and spoilage of such products, which shapes their dual role.

On the one hand, LABs serve as valuable probiotics and the basis for biopreservation, inhibiting pathogens (e.g., *Listeria monocytogenes*) through the production of organic acids, bacteriocins, and other antimicrobial compounds. They are widely used in the production of fermented foods (kefir, yogurt, sauerkraut, sourdough bread), where they not only improve sensory and nutritional properties but also naturally extend shelf life. Research also confirms the antiviral and antifungal activity of their metabolites.

On the other hand, certain LAB strains may cause spoilage, especially in meat and finished products with limited chemical preservatives. For example, *Lactobacillus, Leuconostoc, Carnobacterium*, and *Weissella* species can produce diacetyl, which imparts an "oily" flavor, emit gases that cause packaging to bulge, or form biogenic amines that are hazardous to consumers [1]. Of particular concern are psychrotrophic strains adapted to refrigerated storage and capable of forming resistant biofilms on equipment, leading to persistent cross-contamination.

Modern research confirms that the spoilage or beneficial potential depends on the specific strain rather than on the species. For example, *Lactobacillus sakei* may exhibit both antimicrobial activity and act as a spoilage agent depending on its biotype [2]. This highlights the critical need to move from generalized approaches to strain-specific risk analysis. Modern methods, including metagenomics, metabolomics, and molecular typing, allow not only the identification of "problematic" strains but also the prediction of their behavior in various products and storage conditions.

The aim of this review is to summarize current data on the dual role of LABs in the food industry, emphasizing their ability to act both as biopreservatives/probiotics and as food spoilage agents, particularly in the meat industry. The review aims to systematize knowledge about strain-specific properties, mechanisms of beneficial and adverse effects, and modern control methods, as well as to analyze the pathways of LAB dissemination and persistence in the production environment.

Objects and methods

A systematic review of the scientific literature (1996 to 2023) was conducted using Google Scholar, PubMed, Web of Science, Research Gate, Springer Link, ScienceDirect, Taylor & Francis, and Scopus, as well as Google and other search engines. A total of 105 relevant publications were identified and analyzed using keywords related to lactic acid bacteria, their beneficial properties, and food spoilage.

Classification and characteristics of lactic acid bacteria

Lactic acid bacteria (LABs) are a functionally distinct but phylogenetically diverse group of Gram-positive microorganisms united by a key physiological trait: the ability to produce lactic acid as the primary end product of carbohydrate fermentation [3]. These bacteria are chemoorganoheterotrophs, obtaining energy exclusively through substrate-type phosphorylation during fermentation. Morphologically, the group is represented by both bacillary and coccoid forms. Common features of LABs include Gram-positive staining, do not form endospores (with rare exceptions), immobility in most species [4], and catalase negativity. They demonstrate increased tolerance to acidity, which is their key competitive advantage [5]. LABs have complex nutritional requirements, requiring the presence of amino acids, B vitamins, and minerals [6,7]. In nature, they are widespread in nutrient-rich ecological niches: on plants, in dairy products, fermented substrates, and in the gastrointestinal tract of humans and animals [8]. Their ability to produce organic acids allows them to effectively suppress the growth of competing and potentially pathogenic microflora, which determines their key role in biopreservation practices [9].

The traditional classification of LABs established at the beginning of the 20th century was based on a complex of morphological, physiological, and biochemical characteristics. A fundamental and still valid criterion is the division into homofermentative and heterofermentative types depending on the hexose fermentation pathway [3]. Homofermentative LABs (e.g., the genera *Lactococcus, Streptococcus, Pediococcus*) break down glucose via the glycolytic pathway (Embden-Meyerhof-Parnas), and the end product is predominantly lactic acid. In contrast, heterofermentative LABs (e.g., the genera *Leuconostoc, Weissella, Oenococcus*) use the phosphoketolase pathway, resulting in the formation of lactic acid, ethanol or acetic acid, and carbon dioxide from one glucose molecule [3]. Other important phenotypic criteria include optimal growth temperature, the ability to ferment certain carbohydrates, and salt tolerance [10,11]. However, phenotypic identification is often insufficiently reliable for differentiating closely related species, which has led to a radical revision of LAB taxonomy with the development of molecular genetic methods. Thus, based on DNA hybridization data and phylogenetic analysis, the heterogeneous genus *Streptococcus* was divided into several independent genera: *Streptococcus, Enterococcus,* and *Lactococcus*. A major revision of species initiated in 2020 also affected the largest genus *Lactobacillus*, which was divided into 25 new genera (e.g., *Lacticaseibacillus, Limosilactobacillus*) based on whole-genome sequencing [12].

Therefore, modern taxonomy and identification of LABs are based on a polyphasic approach integrating phenotypic data with the results of genetic analysis [12]. Key methods include 16S rRNA gene sequencing, which is the "gold standard" for species identification, genomic fingerprinting methods such as restriction fragment length polymorphism (RFLP) analysis and randomly amplified polymorphic DNA (RAPD) analysis, as well as whole genome sequencing (WGS), which provides the most comprehensive information for taxonomy and the study of metabolic potential [13].

The application of these methods has allowed to form a modern taxonomic structure and clearly define the key LAB genera of industrial significance. According to the modern classification, the core of the LAB group is the order *Lactobacillales*. Bacillary bacteria of the genus *Lactobacillus* (and newly described genera) are extremely diverse in their metabolic properties and are of great importance in the production of fermented products and as probiotics [3,8,12,14]. Mesophilic homofermentative cocci *Lactococcus lactis* are a key starter microorganism in cheese manufacturing [3]. Thermophilic homofermentative cocci *Streptococcus thermophilus* are one of the essential components of yogurt starter [3]. Obligately heterofermentative cocci *Leuconostoc mesenteroides* are important in the initial stages of vegetable fermentation, and *Oenococcus oeni* is specially adapted to survive in wine and is responsible for biological stabilization [3,11]. Homofermentative cocci of the genus *Pediococcus*, which form tetrads, are highly acid-resistant and are used in the fermentation of plant and meat raw materials [9]. The genus *Bifidobacterium* belonging to the phylum *Actinobacteria* stands apart. Although their metabolic pathways and phylogenetic position are distinct, they are often considered together with LABs in applied contexts [8].

Lactic acid bacteria are the basis of numerous food biotechnologies. Their role is far beyond simple acidification. Through proteolytic and lipolytic activity, they shape the flavor profile of cheeses, fermented meat, and plant products [3]. Bacteriocins produced by many strains serve as natural biopreservatives [9,13]. A special area of research is the use of LABs as probiotics, live microorganisms that benefit the host's health [8,14,15]. Probiotic strains must possess a combination of properties: resistance to gastric juice and bile acids, adhesion to intestinal epithelium, antagonistic activity against pathogens, clinically proven efficacy and safety [14,15]. Thus, lactic acid bacteria represent a classic example of the interplay between fundamental science and practice. The evolution of their classification from phenotypic descriptions to genome-focused approaches has opened up new opportunities for targeted

screening, selection, and safe use of these microorganisms in the food industry, medicine, and agriculture [5,12].

Bioactive compounds of lactic acid bacteria: diversity, mechanisms of action, and application in food technology

LAB bioactive compounds as multifunctional agents

Lactic acid bacteria (LABs) are an integral part of food biotechnology, not only due to their primary enzymatic activity but also due to their ability to produce a wide range of bioactive compounds [16]. These metabolites synthesized during fermentation make a key contribution to the safety, quality, texture, shelf life, and health benefits of final products. The main classes of bioactive compounds produced by LABs are peptides, exopolysaccharides (EPS), bacteriocins, organic acids, and enzymes [16]. The profile and quantity of the compounds produced vary depending on the bacterial species and strains, substrate, and fermentation conditions, opening up vast opportunities for the targeted creation of products with desired technological and functional properties. Thus, LABs act as powerful biotransformers and biofactories of valuable substances.

Main classes of bioactive compounds and their functions in food products

Bioactive peptides formed as a result of proteolysis of raw material proteins (e.g., milk casein) are the most significant from a functional point of view are. These peptides exhibit a variety of physiological activities, including antihypertensive, antioxidant, immunomodulatory, and opioid effects, which determines the prophylactic potential of fermented products [16]. Exopolysaccharides (EPS) secreted by LABs into the environment play a dual role: they improve the rheological properties of products, acting as natural thickeners and stabilizers, and also exhibit prebiotic and immuno-stimulating effects, promoting the growth of beneficial intestinal microbiota [16,17]. Organic acids, primarily lactic and acetic acids, are the main biopreservation agents lowering the pH and creating an unfavorable environment for the development of pathogenic and opportunistic microflora [18]. The accumulation of acids also contributes to the denaturation of proteins and the formation of the characteristic texture of products such as yogurt or cottage cheese. Furthermore, the enzymatic activity of LABs (proteases, lipases, amylases) leads to profound transformations of the food matrix: increased availability of nutrients, accumulation of free amino acids and fatty acids, formation of flavor compounds, and reduction in antinutrients or allergens in raw materials [17]. The combined action of these compounds significantly increases the nutritional and functional value of the original substrates.

Bacteriocins: mechanisms of action and application strategies in biocontrol

A special place among bioactive metabolites is occupied by bacteriocins, peptides synthesized in ribosomes and exhibiting antimicrobial activity primarily against closely related bacterial species [19]. In the food industry, they are considered promising natural biopreservatives for combating spoilage and pathogens (e.g., *Listeria monocytogenes, Staphylococcus aureus*) [20]. Their key advantages include safety for humans (many have Qualified Presumption of Safety (QPS) status), biodegradability, and efficacy at low concentrations [21]. QPS status implies overall safety across all potential uses, and the assessment incorporates four key principles: taxonomy, scientific knowledge, safety profiles, and expected end use [22]. Combination strategies are used to expand the spectrum of activity, particularly against Gram-negative bacteria. The combined use of bacteriocins with ethylenediaminetetraacetic acid (EDTA) is one of the most common strategies currently used to sensitize Gram-negative bacteria. EDTA promotes the destruction of the bacterial outer membrane, enhancing the activity of the bacteriocin against Gram-negative microorganisms, especially *Salmonella enterica* subsp. *typhimurium, Enterobacter aerogenes, Shigella flexneri, Citrobacter freundii, Escherichia coli* O157: H7, *Pseudomonas aeruginosa,* and *Arcobacter butzleri* [23]. Interestingly, small amounts of EDTA, ranging from 10 to 20 mM, are usually sufficient to induce sensitization to bacteriocins [23]. Combination with essential oils (thymol, carvacrol) allows for a reduction in the working concentrations of both agents, minimizing the impact on the sensory properties of the product [24,25]. A study of *Buyssa* essential oil against *Salmonella enterica* subsp. *typhimurium* and *Staphylococcus aureus* showed that the inclusion of nisin significantly reduced the oil concentration required to inhibit both bacteria [26]. The combined use of bacteriocins with mild physical processing methods (high pressure, moderate heat) is being actively studied [27]. The use of protective cultures producing bacteriocins is an environmentally friendly alternative to synthetic preservatives [28,29].

Antiviral potential of LAB metabolites

In addition to antibacterial activity, LAB metabolites demonstrate potential for inhibition of viruses. This effect is studied primarily in the context of its impact on host health, since viruses do not replicate in food products [30]. Mechanisms of antiviral action may include: direct interaction of bacterial cell components or their metabolites with viral particles; blocking of viral receptors on target cells; and modulation of the body's systemic immune response [30,31]. Studies have shown the activity of some lactobacilli strains and their metabolites against rotaviruses, noroviruses, and caliciviruses [30,31], as well as against the human immunodeficiency virus (HIV) [32]. Until now, information on the ability of lactic acid bacteria to kill viruses has focused on their immunomodulatory effect on the host immune response rather than on the direct antiviral action in foods. However, it is hypothesized that the presence of LABs in food indirectly protects consumers from viral infections by blocking receptor sites on host cells and neutralizing viral spread, or by enhancing the immune

system to counteract viral infections after food consumption [31,32]. Consumption of LAB-containing foods may enhance the immune response, indirectly increasing the body's resistance to viral infections [31,33].

Antifungal activity of LABs and its application in biopreservation

The antifungal activity of LABs, directed primarily against filamentous fungi and yeasts, is of great practical interest for the biopreservation of mold-prone foods [34]. The main agents of this activity are organic acids, low-molecular-weight metabolites, and volatile compounds (diacetyl, acetoin) [34,35]. Many strains of the genera *Lactobacillus, Pediococcus,* and *Leuconostoc* effectively inhibit the growth of toxigenic molds such as *Aspergillus, Penicillium,* and *Mucor* [34,36]. Volatile organic compounds capable of diffusing in the airspace of packaging are particularly promising for protecting product surfaces [35]. The antifungal effect is often the result of synergy between several compounds and interactions between different bioprotective cultures, which increases efficiency [37]. The antifungal process may involve interactions between microbial metabolites produced by various bioprotective cultures [38].

Prospects for the use of bioactive compounds from lactic acid bacteria

Bioactive compounds from lactic acid bacteria form a multifaceted and highly effective arsenal of tools for the modern food industry [16]. Their unique ability to simultaneously address the challenges of biopreservation [18,20,27], texture improvement [16,17], enrichment of products with valuable metabolites [16,17], and the manifestation of preventive (probiotic) properties [18,29] makes LABs indispensable agents for the creation of functional foods. Further research should focus on in-depth understanding of the molecular mechanisms of action, optimization of production conditions for target metabolites, and the development of innovative synergistic approaches. Maximizing the potential of these natural biocatalysts will facilitate the development of food technologies within the framework of current concepts of "clean label," personalized nutrition, and sustainability.

Fermentation: biochemical foundations, historical evolution and modern aspects

Fermentation is one of the oldest biotechnological methods used by humanity for the transformation and preservation of food raw materials. It is essentially a process of anaerobic or microaerophilic metabolism, during which microorganisms (bacteria, yeast, fungi) convert carbohydrates and other substrate components into alcohols, organic acids, gases, and a range of aromatic compounds [39]. These biochemical changes have three key functions: significantly increasing shelf life by suppressing the growth of pathogenic and spoilage microflora (biopreservation), improving sensory properties (taste, aroma, texture), and increasing the nutritional value and digestibility of the product through the preliminary breakdown of complex compounds and the synthesis of vitamins.

The history of fermentation dates back over 13,000 years, as evidenced by archaeological finds such as the remains of fermented beverages in stone mortars from the Natufian period [40]. The transition to sedentary agriculture in the Neolithic gave a powerful impetus to the development of these practices. In China, as early as 9,000 to 8,700 years ago, there was a ritual tradition of brewing beer from rice, Job's tears, and tubers, with molds apparently used to saccharify the starch, a principle underlying the production of modern East Asian sourdoughs [41]. In the Middle East, the fermentation of milk led to the development of cheese prototypes. The preservation of plant and animal products by lactic acid fermentation was independently mastered in various regions of the world: from the Roman Empire and Slavic territories to the Himalayas and the Korean Peninsula. A classic example is sauerkraut (and its spicy Korean version, kimchi), which not only ensured long-term storage of plants but, as was later discovered, due to its high content of vitamin C and probiotics, played an important role in the prevention of scurvy and maintaining health [42]. Today, the world's diversity of fermented foods, many of which are part of cultural heritage, numbers in the thousands [43].

Fermented dairy products: from traditional starters to targeted probiotics

Lactic acid bacteria (LABs) are the primary fermentation agents in the dairy industry. Over 260 species of these bacteria are known, performing complex transformations of raw materials. The key process is the fermentation of lactose to form lactic acid, which leads to casein coagulation and curd formation. At the same time, the proteolytic and lipolytic activity of LABs breaks down proteins and fats, generating peptides, free amino acids, and fatty acids that determine the flavor, aroma, and texture of the final product [44].

The evolution from spontaneous fermentation by adding the final product to the use of standardized starter cultures has revolutionized the industry. Modern biotechnology enables the selection of strains with specific properties: high acid production rates, specific flavor-forming properties (diacetyl and acetoin synthesis), and bacteriophage resistance. A particular area of research is the development of probiotic dairy products. Probiotic strains such as *Lactobacillus* spp. and *Bifidobacterium* spp. must not only exhibit targeted beneficial effects (e.g., pathogen antagonism, immune modulation), but also maintain high viability throughout the entire production process and product shelf life, which represents a distinct technological challenge [45].

Fermented plant-based foods: biodiversity and innovation

Fermentation is an effective method for preserving perishable fruits, vegetables, and grains, not only extending their shelf life but also enriching them with nutrients

and bioactive substances [46]. The surface of plant-based raw materials harbors autochthonous microbiota, including low numbers of LABs, but during fermentation, specific consortia are formed. The dominant genera are often *Leuconostoc, Weissella, Pediococcus, Lactococcus,* and *Lactiplantibacillus* (formerly *Lactobacillus*) [47].

Classic products such as sauerkraut demonstrate a staged process: an initial heterofermentative phase involving *Leuconostoc mesenteroides* is followed by a homofermentative phase dominated by *Lactiplantibacillus plantarum*, which ensures optimal acidity and stability. Olive fermentation is a more complex symbiotic process involving LABs and yeasts, with *L. plantarum* and *L. pentosus* playing a key role [48].

A current trend is the development of a market for functional plant-based soft drinks, such as fermented juices. These are positioned as natural, healthy alternatives for consumers with lactose intolerance or milk protein allergies. The use of specially selected probiotic strains (e.g., *Lactobacillus* spp.) allows for the combination of the benefits of plant-based raw materials (vitamins, polyphenols, and fiber) with the beneficial properties of live cultures [49]. Research is focused on identifying new adapted strains, optimizing processes to preserve nutrients, and studying the *in vivo* effects of such products.

Fermentation in bakery: symbiosis of yeasts and lactic acid bacteria

Sourdough bread technology is based on the synergy of yeast and LABs. Yeast (*Saccharomyces cerevisiae*) is responsible for alcoholic fermentation, releasing carbon dioxide to leaven the dough. LABs, a complex of over 70 species (with a predominance of now-reclassified genera such as *Lactiplantibacillus, Fructilactobacillus*, and others), carry out lactic acid fermentation [50,51].

This symbiosis imparts fundamentally different properties to bread. Acidification of the environment (lowering the pH) improves the rheological properties of the dough, slows staling, and inhibits the growth of mold and *Bacillus cereus*, the bacterium that causes "potato disease" of bread. LAB metabolites, lactic and acetic acids, diacetyl, and esters, create a unique flavor profile. In addition, bacterial proteolytic activity increases the availability of amino acids, including glutamate, enhancing the umami flavor, and helps reduce the content of potentially harmful compounds such as acrylamide [52,53]. Traditional Chinese cereal fermentation methods for steamed bread also rely on complex microbial communities to enrich the product [51].

Fermentation of meat and fish products: biopreservation and flavor development

Fermentation of meat and fish is primarily a controlled biopreservation process, an alternative to the use of chemical preservatives. The primary mechanism is the rapid acidification of the substrate through the activity of LAB starter cultures (most commonly *Latilactobacillus sakei* and *Latilactobacillus curvatus*). The accumulation of lactic acid reduces the pH to values (usually below 5.0) unacceptable for the development of most pathogenic and spoilage bacteria, such as *Salmonella* spp. and *Staphylococcus aureus* [54].

Regional differences in technology (e.g., more acidic Northern European products versus less acidic Mediterranean ones) are due to the use of different strains, temperature regimes, and salt concentrations (2–6 %) [55]. In addition to preservation, fermentation makes a decisive contribution to the development of sensory characteristics. The enzymatic activity of LABs and associated microflora (micrococci, coagulase-negative staphylococci, yeasts) leads to profound proteolysis and lipolysis. This causes softening of muscle fibers and the accumulation of free amino acids, peptides, and volatile aromatic compounds creating the characteristic flavor and aroma of dry-cured delicacies [54].

Fish fermentation, one of the oldest methods of fish preservation, also aims to stabilize the product through acidification and enzymatic hydrolysis. This process helps preserve valuable nutrients, including proteins and omega-3 fatty acids, and creates unique traditional products with distinctive flavors [56].

Negative effects of LABs in the food industry

Food spoilage

Lactic acid bacteria (LABs) occupy an ambivalent position in the meat industry, acting simultaneously as agents of targeted biopreservation and as the primary spoilage agents of chilled products. This duality is due to their exceptional ecological plasticity and metabolic diversity. The current understanding of this problem has become more complex with the broadening of plant-based meat analogs. While possessing favorable physicochemical properties for LABs (neutral pH, high moisture), they have become a new niche for their development, including potentially hazardous strains. In light of recent in light of recent research (after 2020), this dual role appears even more complex and is determined not only by species but also by strain-specific metabolic profile, which is being actively studied in the context of clean label and functional food development.

The ecological source and adaptation of LABs in the production environment are the key to understanding the problem of recurrent spoilage. Sources of contamination include both primary raw materials and stable populations within factories. Cross-contamination between raw materials and finished products (e.g., sliced ham) occurs via equipment surfaces and air [57,58]. Psychrotolerant LAB species, which not only survive but also actively grow at refrigerated storage temperatures (0–8 °C), are a particular problem. These species successfully colonize production facilities, adapt, and form stable biofilms, leading to systematic contamination of the final products [58–61]. Similar complex ecosystems, where starter and spoilage

microorganisms coexist, are also characteristic of other food industry sectors [62]. Finished meat products packaged in modified atmosphere or vacuum, which inhibit the growth of competitive aerobic microflora, create ideal conditions for the dominance of psychrotrophic LABs, which cause spoilage [63–65].

An important contemporary aspect is the taxonomic revision of the LAB group. In 2020, phylogenetic analysis led to the division of the heterogeneous genus *Lactobacillus* into 25 new genera, including *Latilactobacillus, Lactiplantibacillus,* and *Levilactobacillus*. This division reflects profound genetic and metabolic differences and explains why closely related organisms may exhibit contrasting technological properties. For example, *Latilactobacillus sakei* may be both a dominant spoilage agent and the basis for protective cultures. Understanding this taxonomy is critical for the accurate identification of contaminants and the selection of beneficial strains. Modern analysis also shifts focus to the bioactive potential of LABs beyond classical lactic acid fermentation. In addition to bacteriocins [66–68], their ability to synthesize other antimicrobial agents (organic acids, hydrogen peroxide, reuterin), texture-improving exopolysaccharides, and even neuroactive substances such as gamma-aminobutyric acid (GABA) is being actively studied, opening up prospects for the creation of functional foods.

The taxonomic diversity of LABs associated with meat spoilage is extremely high and geographically determined. Species belonging to new genera derived from *Lactobacillus* (e.g., *Latilactobacillus sakei, Latilactobacillus curvatus*) are among the most common spoilage agents, causing severe acidification, off-flavor, and slime in various types of meat stored under vacuum or in modified atmosphere [69–77]. The strictly psychrotrophic *Lactobacillus algidus*, first isolated from vacuum-packed beef, poses a particular problem for markets with long-term refrigerated storage [78]. Members of the genus *Leuconostoc*, particularly *L. gelidum* and *L. gasicomitatum*, are responsible for gas and acetic acid production, leading to package bulging, oily odor, and slime formation [59,79–85]. *Carnobacterium* spp. are frequently found in meats with low oxygen levels and play a dual role [80, 86–88]. *Weissella* spp. and *Lactococcus* spp. (e.g., *L. piscium*) are also significant spoilage agents, with the latter often dominating toward the end of shelf life [71,74,80,81,89–92]. Certain species of the genus *Enterococcus* have also been detected in spoiled meat [93,94].

Innovative research in recent years has expanded our understanding of the mechanisms for antagonism of protective cultures. In addition to the classical mechanisms of competitive exclusion and bacteriocin diffusion [66–68], new modes of interaction have been discovered. For example, recent studies have identified a contact-dependent mechanism of pathogen inhibition, in which direct physical contact with the cell of an antagonist bacterium (such as *Lactococcus carnosus*) is required to kill a target cell (e.g., *Listeria monocytogenes*). This mechanism is mediated by a specialized protein, bacteriolysin, and opens up new prospects for targeted biopreservation. Furthermore, the use of LABs to combat fungal spoilage and mycotoxins is actively developing. Many strains are capable of producing antifungal metabolites and adsorbing mycotoxins, making them promising "green preservatives" for protecting a wide range of food products.

The geographic and temperature distribution of spoilage agents shows clear pattern. In cold climates and in global supply chains, obligate psychrotrophic species pose a major problem [78,80,91,92]. Their cold adaptation and high competitiveness make them serious spoilage agents. A key problem is that standard microbiological tests at 30 °C often completely ignore these psychrotrophic populations, leading to underestimation of quality and overestimation of shelf life [95]. Control of these LABs is difficult due to their tolerance to cold, vacuum, modified atmosphere [61,64,83,96,97], and even sodium nitrite [98]. The resistance of many strains to sanitization is aggravated by their ability to form biofilms [99]. Research confirms that psychrotrophic species of *Leuconostoc* and *Lactococcus* are the dominant problem at the end of shelf life of packaged chilled products, demonstrating their persistence [92,100].

Thus, the negative impact of LABs in the meat industry is the result of a complex interaction of factors: the adaptability of psychrotrophic species, the inadequacy of standard control methods [95], the selective action of modern packaging technologies [92], and the formation of stable biocenoses in production. Solving this problem requires a paradigm shift. Prospects lie in the field of precision microbial management: the use of modern molecular methods for monitoring, in-depth study of metabolomics and strain-specific mechanisms of action (including recent ones, such as contact-dependent antagonism), and the development of integrated solutions. These include the creation of "microbial consortia" with targeted properties, combining LABs with other gentle technologies (gentle physical methods, active packaging) within the hurdle technology concept, and thoroughly assessing the safety of each candidate strain, including the absence of antibiotic resistance genes. This approach will not only reduce spoilage but also create safe meat products with an extended shelf life and improved functional properties.

LAB prevalence in the food industry

The prevalence and environmental persistence of lactic acid bacteria (LABs) in the food industry represent a complex problem beyond simple contamination of raw materials. LABs are integral commensals of the production environment, demonstrating high plasticity and the ability to form resident populations on processing equipment, indoor surfaces, and in engineering systems. This environmental adaptation reinforced by resistance to a number of environmental factors and the ability to form biofilms creates a significant risk of recurrent contamination of finished products, which directly threatens the

quality and shelf life, especially for pasteurized and chilled products such as cooked sausages [101]. The key genera of contaminants in the meat processing industry are *Lactobacillus* (particularly *L. sakei, L. curvatus*), *Leuconostoc* (*L. gelidum, L. carnosum*), *Carnobacterium,* and *Weissella* (*W. viridescens*), each of which is associated with specific defects, ranging from acidification and slime formation to color changing and packaging bulging.

The primary source of LABs is the raw material, i.e. fresh meat with an initial contamination level that may reach 10^4-10^5 CFU/g. However, to ensure the microbiological stability of products, secondary contamination and microflora circulation control within the facility is critical. Modern studies using molecular typing methods, such as [62,102], clearly demonstrate the phenomenon of cross-contamination by establishing the genetic identity of strains isolated from the surfaces of processing equipment (e.g., cutting tables) and strains responsible for spoilage of finished sausages. This transfer occurs through several key channels.

Air is one of the most significant and dynamic vectors of spread. Aerosols generated during washing, sanitization, cutting, and slicing serve as a vehicle for viable LAB cells. Bacterial concentrations in the air of production areas may be significant, and general ventilation and air conditioning systems facilitate their migration between different departments, including technologically isolated workshops. A striking example is the detection of *Weissella viridescens* in the air of refrigerated rooms, where this specific spoilage microorganism enters from primary processing areas [62,103,104]. Modern studies of the air environment in meat processing plants confirm that the qualitative and quantitative composition of microbial bioaerosols, including the proportion of LABs, serves as a reliable indicator of the sanitary condition of both individual zones and the entire production facility, allowing for the identification of critical risk points before mass product spoilage occurs.

The surfaces of equipment, tools, walls, and floors, especially in conditions of high humidity and the presence of organic residues, serve as primary reservoirs for the adhesion and subsequent formation of biofilms by resident LAB strains. Areas difficult to access for mechanical cleaning, as well as joints, seals, and drain systems, pose a particular hazard. Personnel, mobile process equipment (trolleys, containers), and inadequately disinfected post-treatment water also act as active carriers of contaminants between relatively clean and dirty areas.

Effective management of these risks requires a shift from reactive control to a preventive strategy based on a comprehensive approach. This includes regular monitoring not only of products but also of critical points in the production environment using modern methods such as quantitative PCR (qPCR) and metagenomic analysis, which enable the rapid identification and tracking of target indicator microorganisms, including key spoilage LABs. Based on monitoring data, sanitization programs (HACCP) should be developed and continuously adapted, taking into account the need to disrupt biofilms and target specific resident populations. Zoning of production flows is also an important element, minimizing the contact of raw materials, semi-finished, and finished products, as well as cross-contamination through personnel and air. This systematic approach, integrating continuous environmental monitoring, validated sanitation procedures, and targeted management of processes, allows for not simply reacting to spoilage incidents, but proactively suppressing the circulation of LABs in the production environment, which is the key to the consistent quality and safety of meat products.

Modern approaches to monitoring and controlling the resident LAB populations

Traditional microbiological control methods based on selective swabs are often insufficiently sensitive to detect and identify specific contaminant strains that form biofilms. Modern strategies are shifting toward the use of molecular methods, such as high-throughput sequencing (metagenomics) and MALDI-TOF mass spectrometry, which enable not only detection but also comparative phylogenetic analysis of microflora from various points along the production chain. This makes it possible to map the distribution of a specific undesirable strain and identify the true source of persistent contamination.

Combating persistent LAB biofilms requires a revision of traditional sanitation protocols. In addition to optimizing cleaning and disinfection regimens to address the need to disrupt the biofilm's extracellular polymer matrix, the use of biocontrol and biopreservation tactics is a promising approach. This involves the targeted colonization of production surfaces or the introduction of competing, safe strains of LABs or their metabolites (bacteriocins) into the product, which will suppress the development of unwanted spoilage microflora [102]. Another relevant area is the study and application of combinations of natural antimicrobial agents, such as essential oils (citrus, clove) and their active components (carvacrol, eugenol), which have demonstrated synergistic effectiveness against LABs and may be used within the framework of the "clean label" concept for surface treatment or in packaging materials [101,103,104].

Thus, the problem of LAB prevalence in the food industry has transformed from a simple issue of raw material contamination into a complex task of managing the microbial ecology of the enterprise. An effective solution lies at the intersection of precise microbiological monitoring, the use of modern molecular tools for strain tracking, the development of innovative sanitization protocols targeting biofilms, and the implementation of proactive biological control strategies. This integrated approach allows not only for the mitigation of consequences but also for the proactive management of microbial risks, ensuring consistent food quality and safety.

Conclusion

The review highlights the fundamental ambivalence of lactic acid bacteria (LABs) in the modern food industry, particularly in the context of the "clean label" trend. This duality manifests itself in their ability to act both as indispensable biopreservatives, fermentation agents, and probiotics, and as key microbial spoilage agents, particularly in the chilled meat sector.

On the one hand, LABs are a powerful biotechnological tool. Their ability to produce a complex of bioactive compounds, i.e. organic acids, bacteriocins, and exopolysaccharides, underlies natural methods for extending shelf life and creating functional foods. The introduction of LAB-based protective cultures offers an environmentally friendly alternative to synthetic preservatives and meets consumer demand.

On the other hand, the high ecological plasticity and adaptive potential of certain LAB strains make them a serious challenge. Psychrotrophic representatives of the genera *Lactobacillus, Leuconostoc, Carnobacterium,* and *Weissella*, adapted to refrigerated storage and modified atmosphere packaging, are dominant spoilage agents. Their ability to form persistent populations and biofilms on equipment leads to persistent cross-contamination and significant economic losses.

A key conclusion is the need to move from generalized approaches to precise, strain-specific microbial management. Modern molecular identification and typing methods (metagenomics, MALDI-TOF MS) allow not only the accurate identification of contaminants but also the tracking of their spread throughout the enterprise. Solving this problem requires a comprehensive strategy, including:

1. Improved monitoring of the production environment with an emphasis on identifying psychrotrophic populations and biofilms;
2. Development and validation of targeted sanitation procedures effective against complex microbial communities;
3. Active implementation of biocontrol methods based on the use of safe antagonist strains or their metabolites;
4. Hurdle technology, where the use of LABs as protective cultures is combined with gentle physical processing methods and active packaging.

Thus, the future of the effective use and control of LABs in the food industry lies in a balanced approach that recognizes and utilizes their beneficial potential while simultaneously applying advanced scientific methods to minimize the associated risks. This will ensure consistent quality, safety, and extended shelf life of products while reducing the use of chemical preservatives.

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