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Review

The Role of Microorganisms and Their Antibacterial Compounds in Food Biopreservation

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Abstract: The increase in the nutritional awareness of consumers has meant that products with high nutritional value, sensory attractiveness, and safety are currently being sought on the market. One of the aspects in which the innovativeness of a food product can be considered is the preservation method. Fermentation is considered one of the oldest methods. In practice, biopreservation is primarily a method of using non-pathogenic microorganisms and/or their metabolites to increase microbiological safety and extend food shelf life. Advances in microbiology and genetic engineering, taking into account various sources of microbiota isolation, have rediscovered the fermentation process and allowed us to obtain innovative functional products. Recently, bacteriocins have gained importance. For many years, they have been applied as biopreservatives in food manufacturing, alone or in combination with other preservatives. The most promising perspective of food preservation seems to be the development of combined systems including natural preservatives (i.e., bacteriocin and lipopeptides), emerging non-thermal technologies, and other methods such as encapsulation nanotechnology and active packaging. In this paper, a narrative review is presented to analyze the most recently published literature regarding the role of microorganisms and microbial produced antibacterial compounds in food biopreservation. New biopreservation technologies as an alternative to artificial preservatives were also discussed.

Keywords: food biopreservation; lactic acid bacteria; bacteriocins; fermentation

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Citation: Sionek, B.; Szydłowska, A.; Kołożyn-Krajewska, D. The Role of Microorganisms and Their Antibacterial Compounds in Food Biopreservation. *Appl. Sci.* **2024**, *14*, 5557. https://doi.org/10.3390/app14135557

Academic Editors: Francesco Cappello and Stefano Burgio

Received: 31 May 2024
Revised: 19 June 2024
Accepted: 22 June 2024
Published: 26 June 2024

1. Introduction

The food offered to consumers must be of appropriate quality and, above all, safe. The food production chain is most often very long. At every stage, from raw materials to consumption, there is a risk of hazards affecting the quality factors (nutritional value, sensory value, etc.) and being a potential cause of food poisoning. For this reason, the basic task of food technology is the use of food preservation methods. Food technologists know many preservation methods: thermal, chemical, physicochemical, and biological methods [1].

The concept of food preservation is understood as a preserving procedure, which involves protecting it against spoilage and health hazards that may arise as a result of the action of microorganisms, enzymes, chemical reactions, and physical phenomena. The purpose of preservation is to stop tissue biochemical processes, prevent the growth and activity of microorganisms, stop chemical and physical changes, protect against the invasion and development of pests, and well as against pollution. A very important task of food preservation methods is to extend the shelf life while maintaining the unchanged product quality and, above all, its safety. It is also a way to prevent food waste during distribution and among consumers' use [2].

Among many traditional methods of food preservation, biological methods are one of the oldest. After many years of searching for novel, innovative preservation methods (high-pressure, ultrasound, pulsating light, etc.), a return to the most "natural" methods has recently been observed [1]. Biopreservation is a method of using non-pathogenic microorganisms and/or their metabolites to increase microbiological safety and extend food shelf life. Both starter cultures and special preservation cultures are used in biopreservation. Starter cultures enable the initiation of fermentation processes. Protective cultures primarily control the growth and production of toxins by microorganisms.

The use of bacteria in food technology has a long history. One of the oldest methods of using microorganisms is fermentation, which is also a traditional method of food preservation. Moreover, fermented products obtain many valued sensory and nutritional properties, e.g., they are easier to digest. Humans have used microorganisms to preserve food from ancient civilizations ranging from Assyria, Babylonia, Egypt, and Persia to the Slavic civilizations. The earliest archeological evidence of fermented beverage production and consumption came from Israeli stone mortars (13,000 BC). Other archaeological proof came from investigations in Qiaotou, China. In human history, the fermentation of milk was a very important step. Archaeological evidence indicates that during the early Neolithic (6500 BC) period, in the Near East, milk was processed by the people. Also in Poland, evidence of dairy residues was found in pottery "cheese-strainers" dated around 5200 and 4900–4800 BC, which suggests milk fermentation for cheese making. There is also evidence of the use of fermentation in ancient Egypt (bread, wine, and beer) [3].

Among bacterial metabolites, the most important preservatives are organic acids (lactic, acetic, and propionic), diacetyl, hydrogen peroxide, carbon dioxide, and exopolysaccharides. In recent years, increasing attention has been paid to bacteriocins, small polypeptide molecules ribosomally synthesized by many species of Gram-positive and Gram-negative bacteria and archaea. Attention is also paid to other substances that may act as biopreservatives in the future, e.g., lipopeptides. They will be an alternative to chemical preservatives.

The aim of the review is to present the potential of microorganisms (bacteria, yeast, and bacteriophages) in modern food biopreservation, with particular emphasis on substances produced by these microorganisms. New biopreservation technologies as an alternative to artificial preservatives and the safety aspects of using these new solutions will also be discussed.

2. The Potential of Microorganisms in Producing Antimicrobial Compounds and Their Role in Food Biopreservation

Food biopreservation is based on the rational use of the antimicrobial potential of naturally occurring microorganisms and their metabolites in food. Bioconservation strategies also involve the use of the antimicrobials of the specific strains of microorganisms or their metabolites obtained from natural sources such as bacteria, fungi, plants, or animals. Natural compounds are more active and safer than synthetic compounds, they can deactivate microorganisms and enzymes without compromising sensory or nutritional properties. They can be incorporated into meat, fruits, and vegetables, as well as edible packaging. The main objectives are to extend shelf life by inhibiting food spoilage and increasing food safety by inhibiting the growth of pathogenic bacteria. The application of natural preservatives by the food industry to a certain extent can minimize chemical processing and reduce the intensity of technological treatments [1].

Traditional methods of food preservation, such as fermentation, cooking, drying, smoking, refrigeration, freezing, canning, pasteurizing, dehydrating, freeze-drying, salting, and pickling, comply with consumer expectations [2]. The rising concern about consumers' "natural", "preservative-free" and at the same time "high quality" food makes food manufacturers look for new technological solutions to meet these market requirements. In general, biopreservation meets these requirements. It is defined as the preservation of food using natural or isolated primary and/or secondary metabolites from sources such as bacteria, fungi, plants, and animals. Examples of biopreservatives include bacteria-derived bacteriocins and lipopeptides as well as oils, plant extracts, or the enzymes of plant and animal origin [3].

Many microorganisms, including probiotic microorganisms, especially lactic acid bacteria (LAB) synthesize various types of biologically active compounds that possess antimicrobial properties [4,5]. Bacteria produce two types of antimicrobial proteins (AMPs), namely bacteriocins that are synthesized ribosomally and non-ribosomally (no structural encoding genes), e.g., ε-poly-L-lysine produced by *Streptomyces albulus* [4]. Their size varies from 10–50 amino acids. Their attributes are low toxicity, thermal stability, and activity over a broad range of pH, which meets the requirements for food processing and preservation [6]. Bacteriocins are the most potent and valuable antimicrobial agents that have attracted the food industry toward their application as food preservatives.

Food processing and preservation require different physicochemical processing. Microorganisms synthesizing antimicrobial compounds encounter sometimes extreme conditions, especially when they are used as a starter culture. They must remain viable throughout food manufacturing to produce enough antimicrobial agents to ensure food preservation. Adjunct cultures can be subjected to various harmful factors appearing during transportation, distribution, and storage. It includes environmental stress factors such as temperature and pH changes, oxidative stress, osmotic stress, nutrients depletion or the impact of chemical preservatives such as salt or nitrate and food additives [7]. Antimicrobial activity is associated with cell growth and can be changed with the altering of environmental conditions [8]. Generally, bacteriocins are produced during the exponential growth phase, and in the stationary phase, the synthesis is limited or stopped. Therefore, the optimal physicochemical conditions and food matrix/medium with substrates, such as carbohydrates, nitrogen sources, vitamins, and salts are essential for microorganism antimicrobial activity and adequate bioactive compound production [9].

3. Antimicrobial Compounds Produced by Bacteria

For centuries, fermentation was commonly used for the transformation of perishable food and beverages into stable and safe food products. Nowadays, they appear to have become an alternative to chemical preservatives and additives. LAB naturally presented in food products as a non-starter ingredient provides a broad spectrum of antimicrobial activity, ensuring food preservation during processing (i.e., traditional fermentation) and storage as well. LAB strains are well-known and widely used in food manufacturing due to their probiotic characteristics, human health benefits, sensory attributes as well as their ability to produce antibacterial chemicals. The appropriate LAB strains selected for various food matrices can be employed as a starter ingredient for purposes of food processing or as an additive to prevent food spoilage. To accomplish the desired effect, the challenge is to keep the viable LAB strains in adequate numbers (>10^6 log/CFU) [10].

According to Ibrahim et al., LAB produce antimicrobials that can be classified into three groups: (a) bacteriocins; (b) organic acids; and (c) other small molecules, i.e., diacetyl, hydrogen peroxide [5]. As a result of fermentation, bacteria produce organic acids such as lactic (*Lactobacillus*), acetic (*Acetobacter aceti*), and propionic acids (*Propionibacterium* spp.), inducing the rapid acidification of the food matrix. LAB is acid-tolerant and the autoacidification of food serves as an antibacterial agent that effectively counteracts many competitive non-acidophile microorganisms, including putrefactive and pathogenic bacteria [2,11].

3.1. Organic Acids and Other Small Molecules

The antibacterial activity of organic acids is due to their passive diffusion across the membrane into the cell, which leads to a decrease in intracellular pH (pHi). The acidification of the cytosol significantly reduces enzyme activity, is genotoxic, and causes protein denaturation, leading to cell death [12]. Organic acid comes from the fermentative metabolism. Thea are also available as commercial products that can be added to food. Other LAB biologically active byproducts are ethanol, enzymes, diacetyl, exopolysaccharides (EPS), carbon dioxide, and hydrogen peroxide [3,13].

Lactic acid is a commonly used chemical preservative that inhibits the growth of both Gram-positive and Gram-negative bacteria. Lactic acid bacteriostatic properties are present even at concentrations of 1–2% and at pH > 5. Lactic acid was discovered in sour milk by Scheele in 1780. On the European Food Safety Authority (EFSA) food additives/preservatives list, lactic acid has the number E270 [14–16].

Acetic acid is used as a preservative in a variety of food products. Acetic acid effectively suppresses the growth and decreases the viability of Gram-positive and Gram-negative bacteria, as well as yeasts and molds. Bactericidal activity occurs at concentrations >0.3% while bacteriostatic can occur at concentrations 0.2%. On the EFSA food additives/preservatives list, acetic acid has the number E260 [14,15].

Propionic acid is a relatively strong acid. Small quantities (0.1–0.2%) inhibit the growth of pathogenic bacteria, fungi, molds, and yeast. Propionic acid reduces the presence of pathogenic microorganisms in dairy and grain products, soft or low-alcohol drinks, and some fresh fruits and vegetables. Added to poultry feed products, it reduces contamination by *Salmonella* spp. and mold formation. On the EFSA food additives/preservatives list, propionic acid has the number E280 [14,17].

Diacetyl effectively suppresses Gram-negative bacteria, yeasts, and, in higher concentrations, Gram-positive bacteria. For years, it has been known as a flavoring compound with the status of GRAS (Generally Recognized as Safe). Its antimicrobial activity was discovered in 1927 [18,19]. Diacetyl is non-toxic; however, it should be noted that volatile diacetyl, when inhaled by humans, can be toxic [20].

Hydrogen peroxide is a by-product of some anaerobic LAB strains. The antimicrobial toxic effect on bacteria, molds, and viruses is through peroxides and free radicals called reactive oxygen species (ROS) containing at least one oxygen atom and one or more unpaired electrons [21].

Carbon dioxide produced by LAB has been shown to inhibit the growth of Gram-positive bacteria and Gram-negative including *Enterobacteriaceae* and *Listeria monocytogenes*. On the EFSA food additives/preservatives list, carbon dioxide has the number E290 [14,22].

Exopolysaccharides (EPS) are high-molecular-weight biopolymers synthetized by LAB. They are classified into two groups: homopolysaccharides (HoPS) and heteropolysaccharides (HePS). LAB produces mostly HePS [23]. EPS are used in the food industry as emulsifiers, stabilizers, thickeners, and gelling agents. Some LAB-derived EPS demonstrated antibacterial activity against *Salmonella enterica* serovar *Typhimurium*, *Escherichia coli*, *Vibrio parahaemolyticus*, *Salmonella typhimurium*, *Staphylococcus aureus*, and *Bacillus cereus* [24–28].

3.2. Bacteriocins

Bacterial metabolites, i.e., purified or semi-purified bacteriocins can also be employed to counteract undesired spoilage or pathogenic bacteria. Bacteriocins are small polypeptide molecules ribosomally synthesized by many species of Gram-positive and Gram-negative bacteria and archaea. Bacteriocin synthesis is encoded in transferable bacteria elements such as plasmids and transposons [28,29]. Bacteriocins are harmful to competing microorganisms of ecological niches. Cytotoxicity can be very specific, dependent on its concentration and the nature of the targeted cell. The spectrum of antibacterial activity is narrow. Generally, the most sensitive species of bacteria are those related to bacteriogenic strains. Bacteriocins were discovered by Gratia in 1925. The first isolated bacteriocin was colicin derived from Gram-negative bacteria *Escherichia coli* [30].

To capture the diversity of many bacteriocins, a few attempts at classification systems were proposed. The first bacteriocin classification was introduced by Klaenhammer in 1993 [28]. The classification proposed by Heng et al. captures all the bacteriocin isolated from the Gram-positive bacteria [31]. Another classification introduced by Arnison et al. divided bacteriocins from Gram-positive and Gram-negative bacteria into two large groups: class I of molecular mass <5 kDa including lanthipeptides, sactipeptides, circular peptides, and glycocins, and class II of molecular mass 6–10 kDa. Bacteriocins of class I compared to class II are more stable to physicochemical factors such as high temperatures and extreme pHs, and more resistant to proteolytic enzymes [32]. Bacteriocins are a diverse and growing group of antimicrobial peptides produced by a wide range of bacteria. Therefore, to assemble available information and better categorize them, open-access databases were created (Table 1).

Table 1. Bacteriocins databases.

Name of the Database	Http Address (Accessed on 21 June 2024)	References
UniProtKB/Swiss-Prot, BAGEL	https://www.uniprot.org?/uniprotkb?query=bacteriocin/	[33]
antiSMASH 2.0	http://antismash.Secondarymetabolites.org	[34]
ADAM	https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4426897/	[35]
BAGEL3	http://bagel.molgenrug.nl	[35]
BUR—Bacteriocins database URMITE	https://drissifatima.wixsite.com/bacteriocins	[36]
NucleBact	https://pubmlst.org/projects/nuclebact	[37]
LABiocin	https://labiocin.univ-lille.fr	[38]
Syngulon	https://syngulon.com	[39]
Bacteriocin	https://aapep.bocsci.com	[40]
BACTIBASE	https://www.re3data.org/repository/r3d100012755	[41]

The primary target for bacteriocins is the cell membrane. Cell membrane disruption is a major antimicrobial mechanism of bacteriocins. They attack bacterial membrane surface charge and membrane fluidity binding by anionic lipids. Cell permeabilization and pore formation cause the efflux of cytoplasm and, in turn, lead to cell death—a bactericidal effect [42–45]. The bacteriostatic activity of bacteriocins is due to the interaction with DNA gyrase, RNA polymerase, and other essential cellular macromolecules. Bacteriocinogenic bacteria are equipped with a protection mechanism against bacteriocins. This protection is ensured by a combined system of efflux pumps transporting bacteriocins outside the cell and by immunity proteins [46,47].

According to the crucial issue that is food safety, the most valuable in the food industry bacteriogenic species are those which effectively reduce the occurrence of spoilage microorganisms and foodborne pathogens. However, they can also be harmful to the beneficial microbiota. Therefore, the selection of bacteriocins should consider that the beneficial microorganism naturally present in various foods (i.e., fermented food) or added as an adjunct culture (i.e., probiotics) ought to be unaffected [47]. On the other hand, the level of bacteriocin or producing bacteriogenic strains should remain at the appropriate level in food to ensure the antimicrobial effect. The antimicrobial activity of bacteriocins can be diminished by physicochemical stresses occurring at different steps of food processing. However, some of them were shown to be stable at low pH and high temperatures, and tolerate a wide spectrum of salt concentrations [48]. Bacteriocins can also be destroyed by proteolytic enzymes synthesized by competitive microorganisms [49]. According to Soltani et al. (2021), the main advantages of bacteriocins in food biopreservation are (1) the lengthening of a food product's shelf life, (2) additional antimicrobial protection during high-temperature food processing and other physicochemical stresses associated with food manufacturing, (3) the risk reduction in spreading foodborne pathogen via food products, (4) the limitation of economic losses due to the reduction in spoiled food, (5) alleviation of food processing treatments along with maintaining food safety and sensory traits as well as with the reduction in food processing-derived losses of vitamins, nutrients, and other beneficial compounds [47]. Bacteriocins can be applied to food as biopreservatives directly in the purified or semi-purified form. Another way to provide them to the food matrix is through the addition of suitable bacterial strains synthesizing bacteriocins.

Bacteriocins can be affected within food matrixes by external harmful physicochemical conditions and by proteolytic degradation. Moreover, bacteriocins added to food or produced in food matrix are sensitive to the proteolytic enzymes of the digestive tract. To maintain its activity in food matrixes as well as in the digestive tract, encapsulation methods are developed and introduced [50]. To improve bacteriocin stability and efficacy, different nanoencapsulation systems were developed, such as metal (gold, silver, palladium), solid lipid nanoparticles, phytoglycogen, chitosan, and nanofibers. Some of these nanotechnologies can be applied in food preservation [51]. For bacteriocins encapsulations nanoliposomes, nanoemulsions, solid lipid nanoparticles, biopolymeric nanoparticles, and nanofibers were successfully used [52]. The promising natural antimicrobial system of bacteriocin encapsulations suitable for food preservation consists of nanoparticle-based vehicles with antimicrobial activity such as chitosan or silver nanoparticles [52,53]. The advantages of such nanotechnology are as follows: (1) the protection of bacteriocins, (2) additive antimicrobial effect, and (3) the development of probably more effective nano-formulated bacteriocins.

Prospects for using nanotechnology to encapsulate bacteriocins in the future show many benefits. Bacteriocins can be nanoencapsulated to make more effective nutricosmetics, medications, and biomedical materials, as well as prolong food shelf life and improve industrialized food safety. As more research is carried out on the molecular stability and controlled release of encapsulated bacteriocin from nanotechnology, these applications will soon become a reality [54].

In relation to the presence of bacteriocins in the environment and their antimicrobial activity, some targeted microorganisms in an evolutionary response can develop resistance mechanisms [4]. The bacteriocin resistance can be acquired or innate (naturally to related resistant strains). The main mechanisms cover the impermeability of cell membrane (1) reduction or loss of bacteriocin binding or insertion, (2) bacteriocin sequestering, (3) bacteriocin efflux pumping, and (4) bacteriocin degradation [55]. Due to the increasing demand for biopreservative development and usage, bacteriocin resistance is a rising concern. Therefore, the significance and mechanisms of bacteriocin resistance need to be extensively explored [56].

Bacteriocins can be applied as biopreservatives in food manufacturing alone or in combination with other preservatives. Due to numerous advantages and the long-term experience of usage nowadays, many bacteriocins are commercially available (Table 2). Bacteriocins and other antimicrobial proteins can be produced by a different microorganism. Screening for microorganism-producing AMPs is a complex process. In this search, genetic analysis and PCR methods are useful. After identification, the next step is purification. Culturing AMP's producer strains is the main method of obtaining them [57]. The progress in technology allows for the chemical synthesis of peptide-based compounds. The chemical synthesis of AMPs, especially the solid-phase peptide synthesis (SPPS) approach, offers many advantages, including the following: pure products, the possibility of molecular engineering modification, and large-scale production [58].

Table 2. Commercial bacteriocins used in food industries according to Pisoschi et al. [1], Soltani et al. [47], Todorov et al. [48], Hirozawa et al. [59], Szabo and Cahill [60], Meena et al. [61], and Cesa-Lunae et al. [62].

Bacteriocin Name	Commercial Product	Application as a Biopreservative	Approval Status
Nisin	Nisaplin® (Danisco, Copenhagen, Denmark), Chrisin® (Chr.Hansen, Horsholm, Denmark) BioSate™, (Chr. Hansen, Horsholm, Denmark) Delvo®Nis (DSM, Delft, The Netherlands), Novasin™ (Danisco, Copenhagen, Denmark)	Dairy, fermented products, fish	FDA, EFSA (E234)
Pediocin PA-1	Microgard™ (Danisco, Copenhagen, Denmark), ALTA™ 2341 (Naarden, Netherlands)	Vegetable and fruits	FDA
Sakacin	Bactoferm™ B-2, Bactoferm™ B-FM (Chr. Hansen, Horsholm, Denmark)	Dairy	FDA
Leucocin A	Bactoferm™ B-SF-43 A (Chr. Hansen, Horsholm, Denmark)	Meat	FDA
Natamycin	Natamax (DuPont™ Danisco® DuPont de Nemours, Inc., Wimington, DE, USA) Delvocid (DSM), (Heerlen, The Netherlands) Natacyn (Eyevance Pharmaceuticals LLC, Fort Worth, TX, USA)	Dairy, meat, fruits and vegetables	FDA, EFSA (E235)

Nisin is a bacteriocin of the structure of polycyclic peptide. It is produced by Gram-positive bacteria such as *Streptococcus* and *Lactococcus*. Nisin has bactericidal or bacteriostatic activity. It is the oldest and most studied bacteriocin. Nisin was discovered in 1928 in milk and has been used in biopreservation since 1950. This means that nisin has a history of being used as a food additive before 1958, which fulfills the criteria of GRAS status [43]. The first approval for its use in foods was established in 1969 by an Expert Committee of Food Additives of FAO/WHO [63]. In 1983, nisin was registered in the European Union for application in food products. In 1988, the FDA accepted nisin as an antimicrobial agent on the list of Direct Food Substances Affirmed As Generally Recognized as Safe [64,65]. Nisin is a bacteriocin of class I. It is thermally stable and does not lose activity in processes like pasteurization and sterilization. At pH 2, it remains active even at 121 °C. As the pH increases, it becomes less heat-stable [43,66]. Now, nisin still meets the criteria for safety and is approved in more than 80 countries. There are two variants, namely Nisin A and Z of the similar, broad range of Gram-positive antibacterial spectrum from species responsible for foodborne illnesses such as *Listeria monocytogenes*, *Staphylococcus aureus*, *Clostridium* spp. and *Bacillus cereus* to beneficial species strains, such as *Lactobacillus acidophilus* and *Lactobacillus plantarum* [59]. Nisin was found to inhibit the growth of *C. botulinum* spores in cheese [67]. In combination with natamycin, nisin inhibits the growth of yeasts and molds [68]. As a biopreservative, nisin is used in various food products, including dairy, meat, seafood, vegetables, and fruits. The spoilage of dairy products is efficiently prevented by using nisin in the purified form or by using live bacteria that produce nisin [69,70]. Nisin-synthesizing bacterial strains, i.e., Lactococci, are used to preserve cheddar cheese [59,71]. On the EFSA food additives/preservatives list, nisin has the number E234 (Table 2) [14].

Pediocins are a group of bacteriocin synthesized by *Pediococcus* strains that act against Gram-positive bacteria including *Listeria monocytogenes*, *Staphylococcus aureus*, *Clostridium* spp., *Bacillus cereus*, *E. faecalis*, and *Clostridium perfringens*. They are thermostable bacteriocins belonging to class II. They are heat-stable at 100 °C for 10 min. The highest stability is achieved at pH 4–6. The heat stability decreases with more alkaline pH. Freezing (−25 °C) does not reduce pediocin activity [72]. Pediocins showed applications in food biopreservation (dairy, meat, vegetables, and seafood) and the medical sector for the prevention of infection. The commercial name of Pediocin PA-1 in the market is ALTA™ 2341 (Table 2) [1,59,60].

Enterocin is a circular peptide synthesized by *Enterococcus* spp. Its bacteriostatic antimicrobial activity is available even in extreme temperatures (activity present after 15 min at 121 °C), pH (at pH range from 3 to 12), and high salt concentrations, and it is effective on bacterial spores in food products [47,73]. Enterocins' antimicrobial effects cover bacteria such as *Clostridium perfringens*, *Clostridium botulinum*, *Listeria monocytogenes*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Escherichia coli*, *Pseudomonas* spp., and *Shigella sonnei* [74,75]. The applications as food biopreservative include fruits, vegetables, rice, seafood, cakes, and creams fruits, vegetables, rice, seafood, cakes, and creams [59].

Epsilon-poly-L-lysine is approved by FDA and in Japan, South Africa, and many Asian countries as a preservative [76].

Natamycin peptide secreted by *Streptomyces natalensis* and *Streptomyces chattanogenesis* has antifungal activity and acts against yeasts and molds. Natamycin, known as pimaricin, was discovered in 1955 [77]. It remains heat-stable even after continuous heating at 100 °C [61]. As a biopreservative, it prevents fungal growth and can be applied for dairy, meat, olives, wines, bakery, and fruit related products. Natamycin is approved by WHO, FDA, and EFSA and has GRAS status [59,61]. On the EFSA food additives/preservatives list, natamycin has the number E235 (Table 2) [14].

Plantaricins are produced by *Lactobacillus* plantarum, which is present in abundance in starter-free cheese synthesized from raw milk. It is heat-stable at 121 °C for 20 min [78]. Plantaricins are effective against *Listeria monocytogenes* [79].

Reuterin are peptides produced by *Lactobacillus* reuteri. They have a broad spectrum of antibacterial activity against Gram-positive (inhibits *Listeria monocytogenes* and *S. aureus* coli growth, *Clostridium* spp. spores and vegetative cells) and Gram-negative bacteria (*S. aureus*, *E. coli*), yeasts, and fungi, and are effective against bacterial spores. Reuterin are water soluble, thermostable, and active in a broad range of pH [80,81].

Lacticins are produced by *L. lactis*, and exhibit antimicrobial activity against *Listeria*, *Bacillus*, and *Clostridium tyrobutyricum*. They were applied in milk and dairy products as biopreservatives [13,80].

3.3. Lipopeptides

Lipopeptides (LPs) are natural antimicrobial agents demonstrating wide-ranging inhibitory properties against bacteria (Gram-positive and Gram-negative strains), fungi, molds, and viruses. They are cyclic peptides mostly synthesized by *Bacillus* spp. divided into three families: surfactin, iturin, and fengycin [82]. The main antimicrobial mechanism of LPs is the destabilization of sensitive microorganisms by the impairment of their cell membrane, resulting in the leakage of cytoplasm, which in turn leads to cell death [83]. LPs, due to high antimicrobial effectiveness and low toxicity, were employed as natural biopreservatives for the conservation of post-harvested perishable vegetables and different fruits (lemon, strawberry, mulberry, table grape, tomato, orange fruits, grapes, and Chinese cabbage), resulting in the extension of the shelf life. Another possible field of the food industry for LP implementation is the biopreservation of aquatic products and marine foods [83]. They were successfully applied by Jiang et al. in the winemaking process for the prevention of fungal contamination [84]. The first discovered lipopeptides were iturins (1950), produced by *B. subtilis* and named after the Ituri Congo region where they were isolated from the soil [85,86].

Iturin effectively inhibits fungi and bacteria and has been commonly applied for fresh fruits preservation (berries, pome fruits). It was demonstrated that iturin reduced the pathogenic *Pseudomonas* and *Vibrio* viability in fish slices and effectively suppressed the growth of spoilage microorganisms in large yellow croaker [87,88].

Fengycin is produced by *Bacillus subtilis.* It has a strong antagonistic effect on filamentous fungi but the activity against bacteria and yeast is weak [89]. Fengycin can be used for the food preservation of fruits (cherries, apples, and peaches) and aquatic products [90].

Surfactin has been shown to inhibit the growth of the microorganisms present in rice and bread, prolonging the product's shelf life [91].

Reports are showing enhanced effectiveness of LPs used in mixtures, i.e., iturin, surfactin, and fengycin. Such combinations were demonstrated to be more potent than single lipopeptide in the preservation of fruits, dairy and aquatic food, which is the result of the widening of the antimicrobial spectrum and a possible synergistic effect [83].

4. Antimicrobial Compounds Produced by Yeasts

Yeasts are a diverse group of microorganisms that can thrive in a variety of challenging environments and subsequently spread throughout both human and environmental ecosystems. Scientists are paying more and more attention to the competitive characteristics against other microbes, and they have suggested that these qualities could be successfully applied in the food biopreservation process [92].

Competitiveness for nutrients and available space, the synthesis and secretion of antibacterial compounds, mycoparasitism and the secretion of lytic enzymes, the formation of biofilms, quorum sensing, the induction of systemic resistance in the host, and the generation of reactive oxygen species are the primary mechanisms of the action of bioprotective yeasts. By preadapting yeasts to abiotic stressors such as sublethal oxidative stress and cold acclimation, one can increase the efficacy of antagonistic yeasts and their ability to perform biocontrol functions under a variety of environmental conditions, hence lowering financial losses [93].

Because of their broad-spectrum antibacterial activity, genetic stability, minimal nutritional needs, and capacity to flourish at low temperatures, yeasts are appealing candidates for biological control. Moreover, yeasts are resistant to oxidative damage and low pH. These characteristics provide credence to the use of yeast as a biological antagonist [94].

There have been a lot of studies carried out on the use of yeasts as biocontrol agents in processed foods like coffee, juices, cheese, dry-cured meat products, and fermented goods, but not much on their antagonistic activity in managing undesired yeasts in the brewing and wine industries or the biological control of postharvest diseases in fruits. Table 3 shows selected examples of the usage of yeasts in food biopreservation [95].

Table 3. Usage of yeast in food biopreservation—selected examples.

Food Product	Strain of Yeast	Action Mechanism	References
Cheese	*M. pulcherrima* LMA 2038	Antifungal and antibacterial inhibitions	[96]
Coffee	*S.cerevisiae* CCMA 1302	Formation of biofilm, volatile organic compounds production	[97]
Apple juice	*R. mucilaginosa*	Competition for nutrients, degradation of the mycotoxin patulin	[98]
Wine	*M. pulcherrima*	Secretion of lytic enzymes	[99]
Fermented cured meat	*Meyerozyma guilliermondii*, *Debaryomyces hansenii*	Degradation N-nitrosamine precursors; offer solution to problems with the high risk of generating nitrosamines such as N-nitrosodiethylamine (NDEA) by processing fermented meat products with nitrites as precursors.	[100]

5. Role of Bacteriophages as Antimicrobial Agents

Bacteriophages (phages), as natural predators of bacteria ubiquitous in the environment, are harmless to humans and animals (because they can multiply only in prokaryotic organisms). They have been identified as future-proof antimicrobials that can allow specific bacterial pathogens to be controlled at every stage of food production [101,102]. Lytic bacteriophages isolated from the environment are used to "attack" pathogenic bacteria and eliminate them from food (or, at least, a significant reduction in their level). The use of bacteriophages in food biopreservation represents a new trend in food technology [103]. There is an increase in the number of bacteriophage preparations approved for use in food [104].

A very big advantage of using bacteriophages as a technological solution is the fact that they do not affect the non-target microflora, which is particularly important in the production of fermented food. Nevertheless, phages still offer excellent food biocontrol options as they do not contain any additives or preservatives in their formulation and several are certified Kosher, Halal, and organic, and have no impact on the sensory, nutritional, and rheological properties of the food [105]. However, the challenges associated with the choice of such a method of ensuring the microbiological safety of food are as the risk of transferring antibiotic resistance between bacteria with the participation of bacteriophages or the possibility of the inclusion of bacterial phage resistance mechanisms [106].

There are many companies registered on the global market that develop and distribute bacteriophage preparations for the food industry. These measures are aimed at combating pathogenic bacteria in the food environment, such as *Salmonella*, *Listeria monocytogenes*, *Escherichia coli* O157:H7, or *Shigella* [107].

6. New Technologies of Food Bioconservation as an Alternative to Artificial Preservation

Generally, biopreservation is based on two principles, namely direct competition with undesirable microorganisms and the production of antimicrobial substances [108]. Meat and meat products are prone to spoilage and contamination by pathogenic microorganisms, and therefore require preservation. For this purpose, physicochemical treatments are widely used. Selected microorganisms, including probiotics, and natural antimicrobial agents inhibit spoilage and can also be effectively applied in meat and fish products as additional or alternative preservatives. Bacteriocins, especially nisin and pediocin, successfully inhibit the growth of *Listeria monocytogenes* and have activity against *Salmonella* spp., *Staphyloccus aures*, and *E. coli* in different meat and meat products [109,110]. In dairy products such as milk, yoghurt, and cheeses, bioconservation was effective. The number of reports confirmed that LAB as a starter or adjunct culture, as well as bacteriocins (nisin, pediocin, lactisin, reuterin, enterocin) are successful in controlling pathogens occurring in dairy products (*Listeria monocytogenes* and *Staphylococcus aureus*). In dairy products, bacteriocins alone do not ensure effective antimicrobial protection due to proteolitic degradation, poor solubility, and uneven distribution. Therefore, LAB strains producing bacteriocins are preferred because of safety, shelf-life lengthening, and sensory quality [70]. The shelf life of fresh-cut fruits and vegetables can also be improved using biocontrol agents, such as LAB, and their metabolites applied after inoculation or in edible coatings. These bacteria can reduce the contamination of fresh fruits and vegetables to pathogens [111].

There are many advantages of food biopreservation. The use of natural microbial preservation can be considered as an alternative or can supplement the physicochemical preservative methods (Table 4).

Table 4. Advantages of food biopreservation and combined methods in comparison with physicochemical preservation according to Barcenilla [108], Soltani [47], Todorov [48], Galvez [8], and Zottola [71].

	Biopreservation	Physicochemical Preservation	Combined Methods
Extended shelf life	X	X	X
Safety	X	X	X
Milder physicochemical processing	X	-	X
Better nutritional value	X	-	X
Better performance	X	-	X
Reduction of chemical preservatives	X	-	X
Avoidance of toxic and cardiogenic compounds	X	-	X
Antimicrobial packaging	X	-	X
Consumer acceptance	X	-	X
Future perspective and development	X	X	X
Inactivation of desirable microorganisms (fermentation cultures, probiotics)	X	X	X
Risk of transferring virulence factors	X	-	X
Development of resistance	X	-	X

Explanatory notes: "X"- present, "-" absent.

The combination of bacteriocins with chemical preservatives offers potential antimicrobial synergistic results. Organic acids and NaCl treatment enhance the antimicrobial activity of most bacteriocins [112]. The antimicrobial synergistic effect of bacteriocins was shown also in a modified atmosphere (CO_2 and N_2) [113].

The market is growing not only for natural preservatives but also for environmentally friendly and biodegradable packaging materials [114].

A common method of applying natural antimicrobial agents to food to extend shelf life is their direct addition and use in an active packaging system [114]. Active packaging is packaging in which additional ingredients have been placed inside the packaging and/or on the packaging in order to increase the efficiency of the packaging system. The task of active packaging is to extend the shelf life of food by actively influencing the packaging and/or packaging components on the packaged product or the environment inside the packaging [115]. The development and application of active packages for foods is a growing research area. Active packaging is a promising technology that actively modifies the internal environment of the food product package by interacting with the food over the storage time. Also, it is defined as an intelligent packaging system that alters and modifies the environment inside the package, and consequently, the state of the food system in order to improve the food quality and extend the shelf life of the product [116]. There are two main methods of using bacteriocins in food-packaging applications: (1) in situ, by incorporating bacteriocin-producing bacteria [117], or (2) ex situ with the addition of purified or semi-purified bacteriocin or bacteriocin-like substances [118,119]. The incorporation of bacteriocins into the packaging of the food product ensures continuous protection against the external impurities and inhibits the development of microorganisms inside the package [120].

Several ways of creating this type of packaging containing bacteriocins have also been developed: (1) including biostatic substances in the structure of the polymer (or paper), constituting the packaging by means of melting, extrusion, or the use of a solvent [120,121], (2) adsorption on the surface of the material of the antimicrobial compound [122,123], and (3) creating covalent or ionic bonds between the polymer and the antimicrobial component, using a polymer with antimicrobial activity, such as chitosan [124–126].

Nowadays, many biodegradable and edible biopolymers are developed, including materials with antimicrobial properties such as chitosan or polylactic acid (PLA). Those natural biopolymers, due to mechanical strength and low toxicity, are suitable for food packaging. Moreover, incorporation into the packaging of bacteriocins, antioxidants, antimicrobial compounds (polyphenols, tanins, flavonoids, gallic and ferulic acid, silver nanoparticles), ROS scavengers, or moisture absorbents can contribute to additional positive effects on food safety and quality [127]. By using antimicrobial materials or the antibacterial qualities of the polymer it is comprised of, antimicrobial packaging can prevent or limit the growth of unwanted microorganisms [128]. The use of postbiotics in active packaging systems may concern a single postbiotic or a mixture thereof. The new packaging techniques give wide possibilities for application in the food industry and are interesting alternatives for plastic and synthetic gasoline polymers. This antimicrobial-combined packaging technology allows for continuous interactive biopreservation achieved by the controlled release of antimicrobial agents delaying the spoilage of packaged food [56].

Another technological solution is to include antimicrobial agents in the active packaging in the form of a mixture of mainly cell-free supernatant (CFS, cell-free supernatant), which is the fluid formed as a result of the centrifugation of liquids after bacterial cell culture. The cell-free supernatant contains a number of low- and high-molecular-weight bacterial metabolites with synergistic antimicrobial activity. Beristain-Bauza et al. report that films supplemented with the *Lactobacillus sakei* NRRL B-1917 cell-free supernatant on beef inoculated with *Escherichia coli* ATCC 25922 or *Listeria monocytogenes* Scott A exhibited antimicrobial activity. Sensory assessment did not show a significant impact of the addition of postbiotics to the packaging material on the quality of stored products [129].

The strategy of combining bioconservation with other preservation methods to achieve a synergistic effect seems to be the most valuable. The combination of preservation methods should consider the physiology and behavior of microorganisms in foods. An integrated intelligent approach to food preservation methods to create safe, stable, and nutritious food is the concept of the effective preservation of foods called hurdle technology [130–132]. For the past 45 years, hurdle technology, initially a combination of physicochemical preservation methods, has evolved into a multitarget preservation approach for food, concerning the physiology and behavior of microorganisms in foods. According to Leistner, the disturbance of the homeostasis of microorganisms is the key phenomenon that may complicate food preservation [133,134]. Bacteriocins can be employed in combination with novel non-thermal preservative methods such as pulsed electric field, high hydrostatic pressure, ultrasound waves or irradiation, and modified atmospheric packaging [135–138]. The synergistic effect of such combinations was confirmed in various food matrices. Bacteriocins can be more effective in influencing the permeability of the outer membrane, thus increasing their effectiveness against microorganisms [2,139,140]. Another promising idea is the genetic modification of the naturally available bacteriocins. Bioengineering offers the creation of new bacteriocins with desired food industry properties, like augmented antimicrobial activity [47]. An example of genetic modification is nisin. The substitution of nisin amino acid generated a novel variant nisin Z, which has better solubility, thermal stability, and a wider range of pH activity along with broadened antibacterial activity against Gram-negative food-borne pathogens like *Shigella*, *Pseudomonas*, and *Salmonella* species. The genetical engineering allowed the production of more effective chimeric bacteriocins within diverse groups, including nisin, pediocins, and enterocins [43]. The recombinant DNA technology enables, for example, the fusion of two genes to generate increased production of more efficacious bacteriocins. Furthermore, there are possibilities of chemical bacteriocin synthesis allowing for the modification of amino acid composition, which could help to find compounds of better properties feasible for food preservation [80].

Another promising approach is the combined use of bacteriocins and bacteriophages as food biopreservatives [141]. In the study of Leverentz et al., phage mixtures were combined with nisin, showing a reduction in more than two log units of the *Listeria* population [142]. Another study by Baños et al. also shows the superiority of a combination of enterocin AS-48 and phage P100 against *L. monocytogenes* in raw salmon and smoked salmon [143].

New technologies of food bioconservation, especially the idea of natural antimicrobial biodegradable packaging, are in concordance with ecological consumers' expectations.

The use of one method of food preservation is associated with different limitations, especially at the industrial level. For example, the excessive use of chemical compounds can create potential health risks, high temperatures can decrease nutrient value and sensory organoleptic quality, or natural bioconservation alone can be insufficient for food preservation due to the low capacity of antimicrobial agent productions. To overcome those limitations, the combinations of different methods, including natural preservatives, are promising. Emerging food-processing technologies offer potential for the wide use of suitable biopreservation. Combining non-thermal food preservation techniques, encapsulation nanotechnology, active packaging methods, and microorganism-derived antimicrobial agents seem to be most promising of future food preservations. The adequate mix of physicochemical processing and preservation methods with biopreservation can be broadened by active packaging methods, ensuring the safety and quality of food products [109]. A novel approach is based on genetically modified organisms. It enables the development of microorganisms suitable for food preservation microorganisms as well as the creation of novel bioactive compounds, especially recombinant bacteriocins with enhanced stability and bioavailability, suitable for their application in different food.

7. Safety Aspects of Natural Food Preservatives

Synthetic compounds are effective food preservatives. Unfortunately, the use of them can be associated with health problems, including carcinogenic and genotoxic effects [144]. For example, nitrates, due to their bacteriostatic or bactericidal effect against pathogens, are commonly used as preservatives in meat products. According to the International Agency for Cancer Research, nitrate or nitrite (ingested) under conditions that result in endogenous nitrosation were classified in group 2A as probably carcinogenic to humans [145]. Reduction or replacement of synthetic hazardous preservatives with natural ones is expected to reduce the health risks for humans [146].

In recent years, the misuse and overuse of antibiotics have resulted in a rise in antibiotic resistance including foodborne pathogens. Moreover, these microorganisms are also more tolerant to food processing and preservation methods. Therefore, it should be proved that natural antimicrobial chemical compounds produced by bacteriogenic strains should effectively control food pathogenic and spoilage organisms. Bacterial strains naturally present in food or as an adjunct culture should be viable during food processing and storage when they are planning to be biopreservatives. The desired antimicrobial effect is guaranteed when both bacterial-derived, biologically active chemical compounds and antimicrobial proteins are present in the food matrix. According to Johnson et al., to ensure food safety, bacteriocins as food preservatives should be as follows: (i.) safe to the consumers and harmless to the consumer's intestinal microflora, (ii.) active with a wide antibacterial spectrum of the bacteriocin against the food spoilage organism, (iii.) resistant to enzymes present in food matrices, and (iv.) thermostable and have activity at wide ranges of pH and salt concentration, for inclusion in a wide range of food systems [44]. Bacteriocins and lipopeptides are generally nontoxic for humans [83]. However, bacteriocinogenic microorganisms can be responsible for transferring and carrying virulence factors. Therefore, their safety and efficacy should be tested in detail and analyzed in appropriate tests and trials. Food safety requires both AMP producers' strains as well as its products, like bacteriocins and lipopeptides, to not be harmful to consumers. [48]. According to Soltani et al., an application for the approval of a new bacteriocin should include the following criteria:

- The identity and chemical composition of the new bacteriocin; this means that the active molecule should be highly purified, and its amino acid sequence must be determined using gold-standard biochemical and molecular techniques;
- The method of preparation and stabilization;
- A statement indicating the appropriate concentration or the amount of bacteriocin proposed for its proper use and the purpose for which it is proposed, together with all directions, recommendations, and suggestions regarding its use;
- An acceptable method of analysis, suitable for regulatory purposes that will determine the final concentration of the bacteriocin in the finished food;
- Data showing the efficacy of the bacteriocin for its intended use;
- Detailed reports on the safety of bacteriocin under the recommended conditions of use; these include acute and subacute toxicity reports and long-term exposure effects; bacteriocins with a history of use in foods might be considered as safe;
- Data on the acceptable residual concentration in the finished food product when the additive or bacteriocin is used according to good manufacturing practice;
- A proposed maximum concentration of the additive or bacteriocin in the finished food product [47].

8. Conclusions

The biological substitute for chemical and physical food preservation techniques, which are typically seen as detrimental to product quality and, in certain situations, detrimental to health, may be found through biopreservation. Overall, the processing, preservation, and safety of food can be improved by the biopreservation of food using bacteriocins, bacteriophages, and endolysins. Many years of experience with the use of nisin confirmed its effectiveness in reducing the occurrence of pathogenic and putrefactive food microorganisms. However, currently, only four of the group of almost four hundred bacteriocins are approved for use in food. It should be stressed that the microorganism's potential for antimicrobial agent production is still unexplored. Further research is necessary to develop bioconservation technologies, especially to implement them into food industrial manufacturing. It is anticipated that bacteriocins, bacteriophages, and endolysins will show to be the biopreservative of the future due to the revolution in genetic technology and the progress of molecular procedures. The main concern is food safety strictly guarded by authorities' regulations. Therefore, all the legal requirements should be fulfilled. Moreover, when developing antimicrobial agents, especially as a result of genetic modification or implementing new food processing technologies, we also have to bear in mind consumer acceptance.

Author Contributions: B.S.: Conceptualization, methodology, software, validation, investigation, resources, data curation. B.S., A.S., D.K.-K.: writing—original draft preparation. D.K.-K.: writing—review and editing. D.K.-K.: formal analysis. D.K.-K.: visualization, supervision. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

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