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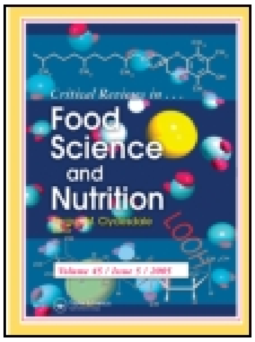

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Bacteriocins: Recent Trends and Potential Applications

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In the modern era, there is great need for food preservation in both developing and developed countries due to increasing demand for extending shelf life and prevention of spoilage of food material. With the emergence of new pathogens and ability of micro-organisms to undergo changes, exploration of new avenues for the food preservation has gained importance. Moreover, awareness among consumers regarding harmful effects of chemical preservatives has been increased. Globally, altogether there is increasing demand by consumers for chemical-free and minimal processed food products. Potential of bacteriocin and its application in reducing the microbiological spoilages and in the preservation of food is long been recognized. Bacteriocins are normally specific to closely related species without disrupting the growth of other microbial populations. A number of applications of bacteriocin have been reported for humans, live stock, aquaculture etc. This review is focused on recent trends and applications of bacteriocins in different areas in addition to their biopreservative potential.

Keywords Bacteriocin, LAB, biological control, fermented food, biopreservation

INTRODUCTION

Food safety is a major criterion for selection of food items by consumers throughout the world. Food-borne diseases are widespread and are one of the major public health concerns both in developed and developing countries. For many years, health hazards associated with pathogenic microorganisms in foods have been recognized. Bacterial pathogens like *Salmonella enteritidis, Eschericia coli* are reported to be the cause of nearly 75% outbreaks of food-borne illness. Various control measures including use of chemicals have been reported to inhibit/killing of the bacteria in food products. Use of chemicals may lead to modification of composition, nutritional, and organoleptic properties of the food items and can also lead to toxicity to humans. Thus, more efforts are being made by People and Government all over the world to improve food safety. Use of naturally produced compounds such as bio-preservative/antibacterial agents has, therefore, gained importance in the food industry, especially in ready-to-use products as compared to the food preserved using chemical agents.

Bacteriocins are antibacterial peptides or proteins which may be bactericidal or bacteriostatic in nature. A number of bacteriocins from gram-positive bacteria have broad spectrum inhibitory activity. Toxicity, processing, stability, broad spectrum inhibition activity, effect on food properties, and a thorough understanding of their biochemical and genetic properties are some of the important parameters considered during the application of bacteriocins in food (Parada et al., 2007). Bacteriocins can also be used for those products that cannot be sterilized by thermal treatment. Bacteriocins from Lactic acid bacteria like *Lactococcus, Streptococcus, Pediococcus, Lactobacillus* are of special interest as they are considered as GRAS and commonly used for the production of feremented foods (Parada et al., 2007; Stoyanova et al., 2007; Ahmed et al., 2010).

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MICROBIAL PRODUCTION OF BACTERIOCINS

Microorganisms

As bacteriocin show inhibitory activity against the closely related strains, therefore, their isolation from different sources is quite important. Numerous microbial strains of Eubacteria and Archaea have been isolated from different sources including food, animals, plants, and clinical samples (Sharma et al., 2006; Silkin et al., 2007; Shin et al., 2008; Rashid et al., 2009; Zheng et al., 2009; Belgacem et al., 2010; Kumar et al., 2010) taking into consideration the application of bacteriocins (Table 1). Some common examples of bacteriocins are nisin (*Lactococcus* sp.), pediocin (*Pediococcus* sp.), lactocin (*Lactobacillus* sp.), enterocin (*Enterococcus* sp.), e*tc.* Generally, bacteriocins from Lactic acid bacteria are of major focus as they inhibit the pathogenic microflora and play a role in selective fermentation of the food product along with its shelf life extention. Wide varities of bacteriocins including nisin with broad or narrow spectrum of inhibition have been isolated from the food grade Lactic acid bacteria and easily introduced as natural food preservatives (Cotter et al., 2005). Bacteriocins of Gram-positive bacteria are as abundant and more diverse as that of Gram negative bacteria (Jack et al., 1995).

Production of Bacteriocins

Wide varieties of media including basal medium, BHI (Brain Heart-Infusion) broth, buffered peptone, lactose broth, litmus milk, MRS (de Man, Rogosa and Sharpe) medium, Mueller-Hinton broth, nutrient broth, skimmed milk and soy milk have been used for the production of baceteriocins (Verschuere et al., 2000; Houlihan and Russell, 2006; Motta et al., 2008; Sawa et al., 2009). A number of LAB strains were grown and maintained in MRS medium (Hosseini et al., 2009). To optimize the fermentation process of the bacteriocin-production, especially to avoid substrate inhibition, strains were shifted from batch to fed batch technique. Rehaiem et al. (2011) proposed the model for the production of entercin A during realkalized fed batch fermentation in MRS medium by *Enterococcus faecium* MMRA. Anthony et al. (2009) used response surface methodology with composite rotary design for optimization of fermentation medium. Supplementation and replacement of medium nutrients with component like spices (curry, pepper, garlic, and rosemary) were demonstrated for possible application in food preservation. In order to make the production of bacteriocin commercially viable, a number of industrial by-products have also been reported. Sugar molasses, milk whey, mussel processing wastes, whey medium are also investigated for the bacteriocin production (Guerra and Pastrana, 2002). The influence of temperature, pH and incubation period on the production of bacteriocin has been investigated by a number of workers (Pai et al., 2008; Anthony et al., 2009). Maximum specific activity of bacteriocin was reported using *Bacillus licheniformis* AnBa9, isolated from slaughter house waste samples, with lactose (17 g/l, w/v) and NH_4NO_3 (12.5 g/l, w/v) using Response surface methology

Table 1 Different bacteriocins and their producer strains (Reproduced with permission from Nagao et al., 2006)

Producer strain	Bacteriocin produced	Reference
Genus Lactobacillus		
Lb. casei CRL 705	Lactocin 705	Graciela et al., 1995
Lb. acidophilus IBB801	Acidophilin 801	Zamfir and Grosu-Tudor, 2009
Lb. amylovorus DCE 471	Amylovorin L471	Callewaert et al., 1999
Lb. bavaricus MI401	Bavaricin A	Larsen et al., 1993
Lb. brevis SB27	Brevicin 27	Benoit et al., 1994
Lb. buchneri LB	Buchnericin LB	Yildirim, 2001
Lb. casei JCM	Crispacin A	Tahara and Kanatani, 1997
Lb. delbrueckii ssp. *lactis*	Lacticin	Takahiro et al., 1991
Lb. fermentum L23	L23	Pascual et al., 2008
Lb. gasseri LF221	Acidocin LF221 B	Majhenic et al., 2004
Lb. helveticus 481	Helveticin J	Joerger and Klaenhammer, 1986
Lb. johnsonii	Lactacin F	Abee et al., 1994
Lb. paracasei BGBUK2-16	217	Lozo et al., 2004
Lb. paraplantarum C7	Paraplantaricin C7	Lee et al., 2007
Lb. pentosus	Pediocin TV35b	Okkers et al., 1999
Lb. plantarum	ST194BZ	Todorov et al., 2006
Lb. reuteri LTH 2584	Reutericyclin	Ganzle et al., 2000
Lb. rhamnosus	Lactocin 160	Li et al., 2005
Lb. sake	Sakacin P	Moretro et al., 2000
Genus : Enterococcus		
E. durans L28-1	Durancin L28-1A	Yanagida et al., 2005
E. faecalis	Enterocin MR99	Sparo et al., 2006
E. faecium LR/6	Enterocin LR/6	Kumar et al., 2010
E. mundtii NFRI 7393	Mundticin KS	Kawamoto et al., 2002
Genus : Lactococcus		
L. garvieae	Garviecin L1-5	Villani et al., 2001
L. lactis QU 4	Lactococcin Q	Zendo et al., 2006
Lactococcus sp. strain QU 12	Lactocyclicin Q	Sawa et al., 2009
Genus : Bacillus		
B. cereus Bc7	Cerein 7B	Oscariz et al., 2006
B. coagulans I4	Coagulin	Marrec et al., 2000
B. licheniformes	Lichenin	Pattnaik et al., 2005
B. pumilus WAPB4	Pumilicin 4	Aunpad and Na-Bangchang, 2007
B. subtilis	Subtilosin A	Kawulka et al., 2004
B. thuringiensis NEB17	Thuricin 17	Gray et al., 2006
Genus : Streptococcus		
S. bovis HC5	Bovicin HC5	Mantovani et al., 2002
S. cremoris	Lactostrepcin 5	Zajdel et al., 1985
S. faecalis	AS-48	Galvez et al., 1986
S. mutans	Mutacin B-Ny 266	Mota-Meira et al., 1997
S. salivarius 20P3	Salivaricin A	Ross et al., 1993
S. thermophilus ACA-DC 0040	Thermophilin T	Aktypis et al., 2007
S. uberis	Uberolysin	Wirawan et al., 2007
Genus: Leuconostoc		
Leu. carnosum	Carnocin 54	Schillinger et al., 1995
Leu. gelidum	Leucocin A	Van Belkum and Stiles, 1995
Leu. mesenteries	Mesenterocin 5	Daba et al., 1993
Leu. mesenteroides ssp. *dextranicum* ST99	Mesentericin ST99	Todorov and Dicks, 2004

(Continued on next page)

Table 1 Different bacteriocins and their producer strains (Reproduced with permission from Nagao et al., 2006) *(Continued)*

Producer strain	Bacteriocin produced	Reference
Genus : Pediococcus		
P. acidilactici F	Pediocin F	Osmanagaoglu et al., 1998
P. damnosus NCFB 1832	Pediocin PD-1	Green et al., 1997
P. pentosaceus Iz3.13	Pediocin Iz3.13	Bagenda et al., 2008
Genus : Carnobacterium		
C. divergens V41	Divercin V41	Metivier et al., 1998
C.maltaromaticum UAL307	Carnocyclin A	Martin-Visscher et al., 2008
C. piscicola 213	Carnocin KZ 213	Saint-Hubert et al., 2009
Genus : Staphylococcus		
S. aureus KSI1829	Bac 1829	Crupper and Landolo, 1996
S. epidermis K7	Epilancin K7	Van de Kamp et al., 1995
S. warneri FM20	Warnerin 20	Kurniasih and Ray, 2000
Genus: Others		
Bifidobacterium bifidum NCFB 1454	Bifidocin B	Yildirim et al., 1999
Brevibacterium linens OC2	Linenscin OC2	Maisnier-Patin and Richard, 1995
Brochothrix campestris ATCC 43754	Brochocin-C	McCormick et al., 1998
Butyrivibrio fibrisolvens AR10	Butyrivibriocin AR10	Kalmokoff et al., 2003
Clostridium beijerinckii ATCC 25752	Circularin A	Kemperman et al., 2003
Escherichia coli	Microcin J25	Blond et al., 1999
Haloarchaeal strain S8	Halocin S8	Prince and Shand, 2000
Haloferax gibbonsii	Halocin H6	Torreblanca et al., 1989
Haloferax mediterranei R4	Halocin H4	Cheung et al., 1997
Propionibacterium thoenii P126	Jensiin G	Ekinci and Barefoot, 2006

was reported while maximum production with medium containing yeast extract (45 g/L) and NaCl (4.5 g/L) was observed. Alkaline conditions (pH 8.0) and comparitively higher temperature (43°C) were reported to be optimum for maximum production (Anthony et al., 2009), while glycerol (0.5%, w/v); yeast extract (0.5%, w/v), NaCl (3.4 M) at 45°C temperature and pH 7.5 were reported as optimized parameters for the production of halocin from halophilic Sech7a, isolated from a solar saltern (Pai et al., 2008). Thermotolerant LAB (TLAB), which can efficiently produce stable bacteriocin at temperature more than 40°C, can be advantageous as compared to mesophilic LAB and their bacteriocin biosynthesis is more susceptible to high temperature. The bacteriocins from different bacterial strains and their properties have been summarized in Table 2.

Bacteriocin Assays/Methods for Bacteriocin Estimation

The inhibitory activity of bacteriocin is determined by agar-spot assay, agar-well/disc assay as well as spot-on-lawn assay with cell free supernatant of the screened culture (Thakur and Roy, 2009). For agar-spot assay, the bacteriocin producing strain is placed in the centre of agar plate. After overnight incubation, the soft agar containing indicator bacterial culture is poured over it (Campo et al*.,* 2001; Bali et al., 2011). In case of the agar-well assay, the well is created in the centre of the media containing bacterial lawn of indicator strain in which the crude bacteriocin is added (Todorov et al., 2004), whereas in case of agar-disc method, a filter paper disc saturated with the bacteriocin is placed in the centre of the indicator bacterial lawn. Schillinger and Lucke (1989) used spot-on-lawn assay, a test in which indicator culture at the early exponential growth phase was mixed with soft agar and poured on an MRS agar plate. Each culture supernatant was dropped onto the solidified soft agar. The plates were incubated and bacteriocin inhibition was indicated by a clear zone in the soft agar layer.

CLASSIFICATION AND CHARACTERIZATION OF BACTERIOCIN

Broadly, bacteriocins are classified on the basis of their molecular weight and structure into the following classes (Gillor et al., 2008):

Class I: Heat stable, Lantibiotics, or modified peptide chains (Figure 1), having unusual thioether amino acids i.e. Lanthionine (Lan) and Methyllanthionine (MeLan), generated by posttranslational modifications forming covalent bridges in between the specific amino acids (Twomey et al., 2002). Based on structure, bacteriocin of Class I have been subdivided into Subclass Ia which includes relatively elongated flexible positively charged peptides whereas Class Ib includes globular, rigid, and either negative charged/no net charge peptides (Klaenhammer, 1993).

Class II: Nonlantibiotics, small, unmodified/minimally modified and heat stable bacteriocins (Drider et al., 2006). Based on amino acids sequence alignments, Class II has been subdivivded into Subclass IIa which includes antilisterial pediocin like bacteriocins, Subclass IIb having two-peptide (Figure 2), and subclass IIc includes other peptide bacteriocins like circular bacteriocins (Figure 3).

Class III: Large and heat labile bacteriocins with molecular masses of > 30 kDa (Joerger and Klaenhammer, 1990).

Class IV: Heat stable molecules complexed with lipids and carbohydrates (Heng et al., 2007).

Bactibase

BACTIBASE, a data repository of bacteriocin natural antimicrobial peptides, is developed by the Functional Proteomics & Alimentary Bio-preservation Unit at Institute of Applied Biological Sciences Tunis (ISSBAT), Tunisia in collaboration

Table 2 Sources of bacteriocin production and their characteristics

Microorganism	Optimum temperature (°C)	Optimum pH	Bacteriocin characteristic	Reference
Enterococcus faecium LM2	37	Noncontrolled	Broad pH resistance, heat stability	Liu et al., 2011
Enterococcus faecium PC4.1	30	NA	Stability in harsh conditions and free f	Hadji-Sfaxi et al., 2011
Lactococcus sp. *strain* QU12	30	5.6	High level of protease resistance, heat stable	Sawa et al., 2009
Lactobacillus plantarum KC21	10–45	5-9	Probiotic properties, acid and bile tolerant	Lim and Im, 2009
Lactococcus lactis	37	NA	Amino acid sequence is highly similar to that of nisin	El-Shafie et al., 2008
Carnobacterium maltaromaticum UAL307	25	NA	Multi bacteriocin producer, stable at wide range of temperature and pH, unaffected by a variety of proteases	Martin-Visscher et al., 2008
Pediococcus pentosaceus Iz3.13	30	5.0	Heat stable with strong antilisterial activity, active at wide pH range (2-8)	Bagenda et al., 2008
Lactobacillus delbrueckii, L. curvatus, L. coryniformis	25–37	5-8	Probiotic properties such as acid tolerance, bile salt tolerance, antimicrobial activity against food borne pathogens, β-galactosidase activity, antibiotic susceptibility and cholesterol assimilation	Reddy et al., 2007
Bacillus pumilus	37	8	Heat stable upto 121°C, activity against Anti methicillin resistant *Staphylococcus aureus* (MRSA) and vancomycin-resistant *Enterococcus faecalis* (VREF)	Aunpad and Na-Bangchang, 2007
Lactobacillus paraplantarum C7	25	4.5	Retain 90% activity after 10 min at 100°C, stable in pH 2-8	Lee et al., 2007
Lactobacillus paracasei subsp. *paracasei* BGSJ2-8	30	5	Exhibit aggregation phenotype, heat stable, retain 25% activity after autoclaving	Lozo et al., 2004
Enterococcus faecium AL41	30	5	Heat stable, broad antimicrobial spectrum and anti listerial	Marekova et al., 2007
Streptococcus thermophilus ACA-DC 0040	30	6.2	NA	Aktypis et al., 2007
Lactobacillus animalis C060203	33	6	Wide inhibitory spectrum against gram positive bacteria, high bacteriocin production in broth containing surfactants	Chen and Yanagida, 2006
Lactobacillus CA44	22–27	4–5	Heat stable	Joshi et al., 2006
Lactococcus lactis	30–37	11	Heat stable, high pH tolerant, broad spectrum activity against Gram positive bacteria	Mitra et al., 2005
Lactococcus lactis C7	30	6.5	Activity same as that of nisin	Moonchai et al., 2005

(na: not available).

with Nutraceuticals and Functional Foods Institute (INAF), Laval University, Canada (http://bactibase.pfba-lab-tun.org/main.php). The current release of the BACTIBASE dataset (version 2, July 2009) comprises 31 genera of bacteriocin sequences from 156 Gram-positive organisms and 18 of Gram-negative organisms with lactic acid bacteria constitute major group of producers of 113 bacteriocins (Hammami et al., 2010). This web-based platform is under continuous development and presently provides well documented, calculated or predicted information for physiochemical properties, data structure, and taxonomic information, producer organisms, target information of 210 bacteriocins produced by both Gram-positive and Gram-negative bacteria (Pascual et al., 2008). This tool helps in easy retrieval, via various filters, of sets of bacteriocins for detailed analysis of a number of microbiological and physicochemical data. As per database, the peptide length among the bacteriocins of Gram-positive organisms varies from 20 to 60 amino acids (84% of cases while Gram-negative bacteriocins have a very broad range of lengths, the longest (BAC127) being 688 amino acid residues. Bacteriocin Genome Location (BAGEL) is web-based bacteriocin mining tool which helps to determine the presence of bacteriocins gene from a (non-annotated) genbank file based on a database containing information of known bacteriocins and adjacent genes involved in bacteriocin activity (http://bagel2.molgenrug.nl/).

MOLECULAR CHARACTERIZATION OF BACTERIOCIN

Bacteriocins have been characterized at the molecular level and it is known that the genetic information for bacteriocin production is often associated with transferable elements such as conjugative transposons or plasmids (Abo-Amer, 2007). This natural association can be exploited to facilitate heterologous bacteriocin production. The production of the unmodified peptide bacteriocins needs a set of minimum four genes which may or may not be located on the same transcription unit. These genes are:

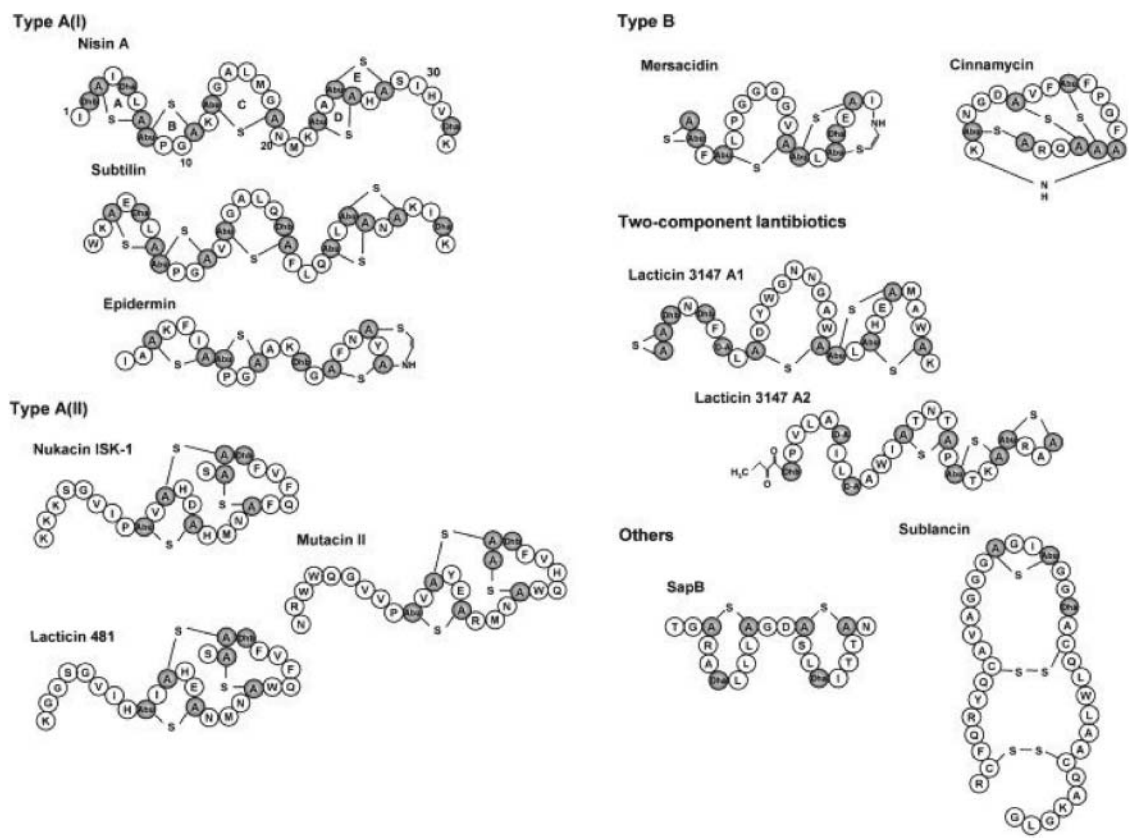

Figure 1 Structure of some lantibiotics. (Reproduced with permission from Nagao et al., 2006).

the structural gene which encodes the preprobacteriocin, an immunity gene, which encodes a protein that protects the producer organism against its own bacteriocin, a gene which encodes a dedicated membrane-associated ABC transporter, and a gene which encodes an accessory protein essential for externalization of the bacteriocin. The N-terminal leader sequence of the inactive pre probacteriocin is cleaved-off by the proteolytic activity of ABC transporter protein leading to its activation (Herranz et al., 1999). An increasing number of LAB genomes have been partly or completely sequenced and in several cases, novel bacteriocin-related genes have been identified in their genomes (Altermann et al., 2005). A 60 kb conjugative plasmid of *L. lactis* DPC3147 contains genes that are required for production of lantibiotic lacticin 3147 which has been transferred to a wide variteis of commercial starter strains by nonrecombinant method (Coakley et al., 1997). In certain cases, bacteriocin genes have been found in the genomes of nonbacteriocin producers normally as incomplete sets of genes or containing mutated genes (Moretro et al., 2005). A number of bacteriocins are being reported from diverse environmental samples, however, characterization of genetic systems responsible for coding and their regulation need to be explored (Liu et al., 2012). Possibilty of biotechnological application of these genes via cloning in suitable hosts could be possibility for future research.

MODE OF ACTION

Different modes of action of bacteriocins have been reported in literature. Class I bacteriocins i.e. lantibiotics binds to target molecules usually Lipid II, the main peptidoglycan subunit transporter from cytoplasm to cell wall and prevents accurate cell wall synthesis. Further, they get inserted in cell membrane and lead to pore formation followed by cell death (Hsu et al., 2004). Class II bacteriocin peptides, with the help of its amphiphilic helical structure, get inserted into the membrane of the target cell causing permeabilization and depolarization by leaking of ions and/or a decrease in intracellular ATP concentration (Bendali et al., 2008). Class III bacteriocins i.e. bacteriolysin (e.g. Lysostaphin) lyse the target cell by cell wall hydrolytic activity (Johnsen et al., 2004). Mostly bacteriocins are synthesized as pre-peptides that are biologically inactive. During their export, N-terminal extensions, called leader sequences, are cleaved off to generate biologically active peptides and transferred across the cytoplasmatic membrane by adenosine triphosphate-binding cassette transporters (ABC transporters) and their accessory proteins (Martin et al., 2007). However, some class II bacteriocins, such as enterocin P, having N-terminal extensions of the so-called *sec*type (signal peptide), which are cleaved-off proteolytically along with bacteriocin externalization by the secretory pathway is called

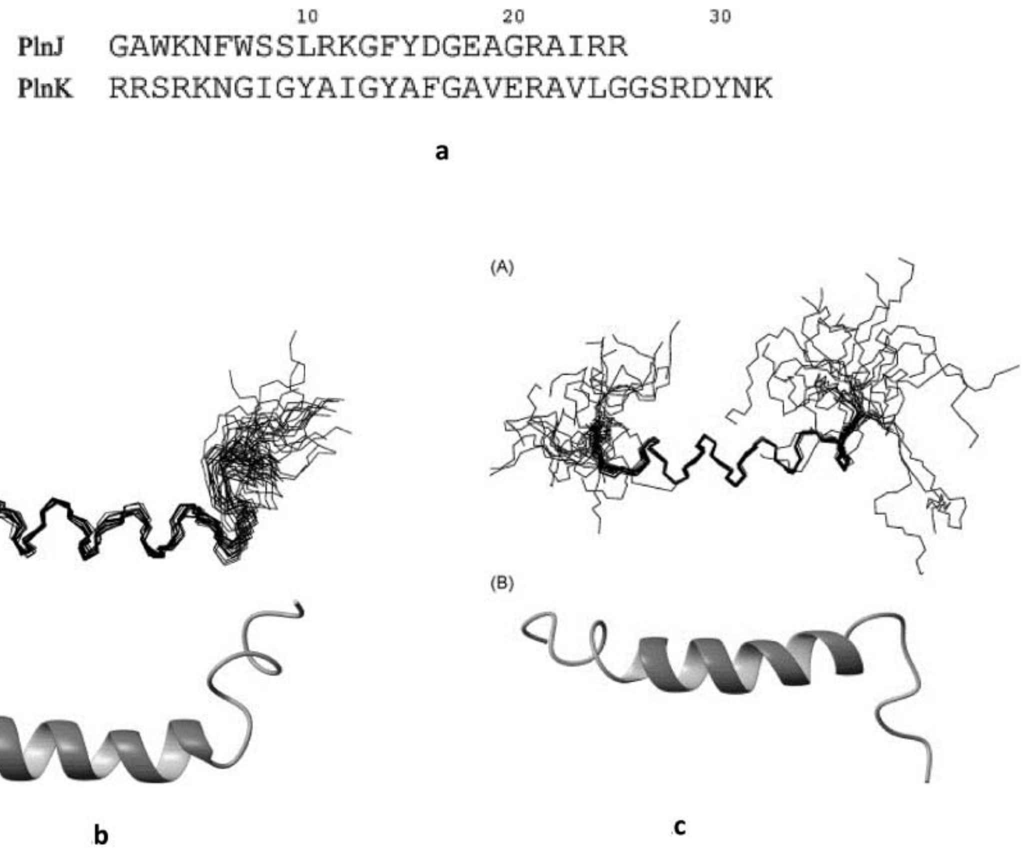

Figure 2 (a) Amino acid sequences of PlnJ and PlnK. (b) The NMR structure of PlnJ. (A) Ensemble of the 20 best structures of PlnJ in DPC-micelles, superimposed over the determined α-helix, residues 3–15. (B) Cartoon drawing of PlnJ in DPC-micelles. The N-terminal is to the left in both figures. (c) The NMR structure of PlnK. (A) Ensemble of the 20 best structures of PlnK in DPC-micelles, superimposed over the determined α-helix, residues 9–24. (B) Cartoon drawing of PlnK in DPC-micelles. The N-terminal is to the left in both figures. (Reproduced with permission from Rogne et al., 2009).

sec-dependent pathway (Gutierrez et al., 2006). Yoneyama et al. (2009) demonstrated new antimicrobial mechanism for the action of Lacticin Q bacteriocin and proposed novel model of "huge toroidal pore." Thus, bacteriocin are found to have bactericidal/bacteriostatic action and is affected by various factors including dose, level of purity, indicator/pathogenic microbes physiological conditions, and environmental factors (Cintas et al., 2001; Deraz et al., 2007; Juodeikiene et al., 2012).

APPLICATIONS OF BACTERIOCINS IN FOOD PROCESSING

Role of bacteriocins/cultures in preservation of food has been widely reported in literature either individually or in combination with other preservation methods, such as heat treatment, high pressures or modified atmosphere packaging (Allende et al., 2006; De Vuyst and Leroy, 2007; Keymanesh et al., 2009; Abriouel et al., 2010). Pure or mixed cultures of bacteriocin-producer lactic acid bacteria and bacteriocin produced by them can be used as protective system against common food spoilage bacteria and pathogens. Application of such cultures may lead to improvement in food quality and sensory attributes through controlling adventitious flora and inducing cell lysis. Bacteriocins have been discovered in cured meats, milk, and cheese, salad dressing, and soybean paste. To preserve and stabilize various kinds of food including fermented dairy products, mayonnaise-type spreads, cream, cheese products, meat or vegetable compositions, whey from nisin-producing cultures is well documented (Nauth et al., 2000; Nauth and Lynum, 2000a, 2000b).

Dairy Industry

Bacteriocins have wide applications in dairy industry especially during the fermentation of the products. Nisin from *L. lactis* and Pediocin PA1 produced from *P. acidilactici* PAC1.0 has found their application in dairy industry. Ryan et al. (1996) reported the application of lacticin 3147 producing transconjugants to control nonstarter Lactic acid bacteria in

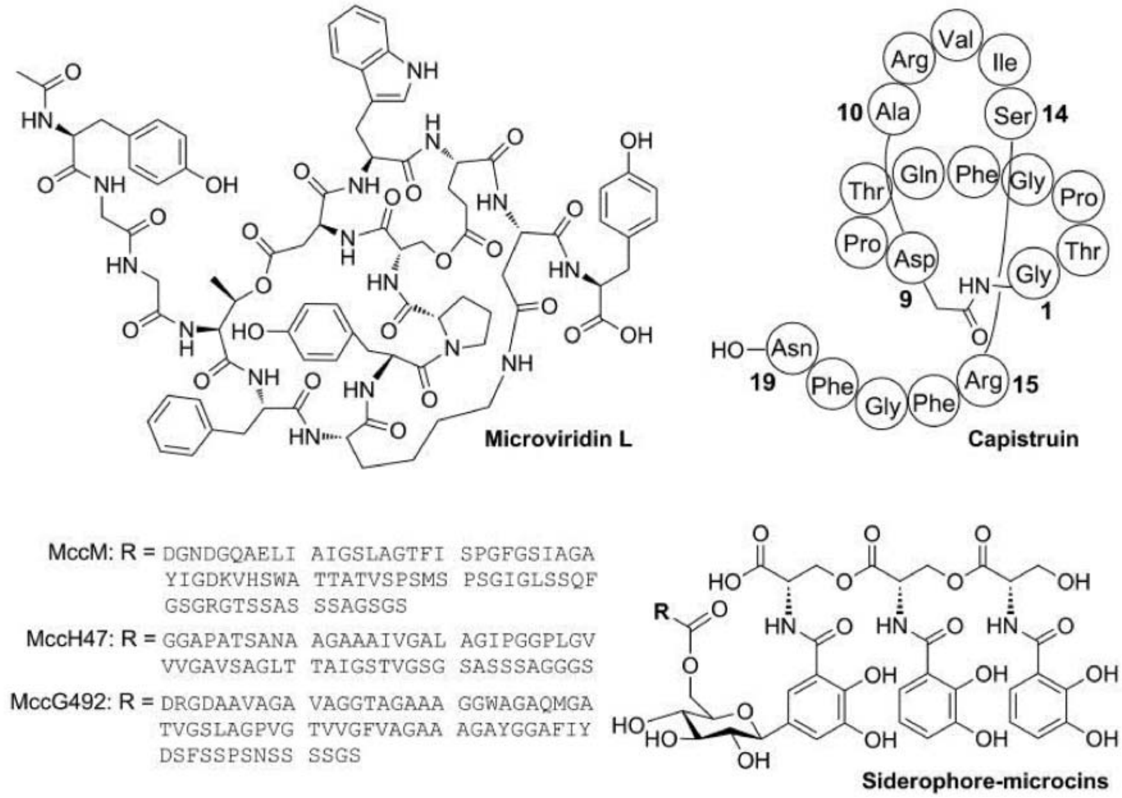

Figure 3 Ribosomal peptides discovered by genome mining containing lactones and lactams or -terminal siderophores. (Reproduced with permission from Velásquez and van der Donk, 2011).

cheese. Addition of Lactococcin ABM helps in early lysis and release of intracellular enzymes from starter culture and helps in early ripening of Cheddar cheese (O'Sullivan et al., 2002). Use of bacteriocin producing starter cultures is advantageous in protecting fermented foods from transmission of food-borne pathogens as compared to starter cultures lacking bacteriocins. Secondary cultures with bacteriocin producing potential may also contribute to fasten the ripening of dairy products by killing microbes in the primary starter culture.

Propionicin PLG-1 from *P. thoenii* P127 is effective against propionibacteria (commonly used as starter culture in Swiss type cheese and also found on human skin), as well as many gram-positive, gram-negative bacteria and few fungi including *Listeria monocytogenes*, *Pseudomonas fluorescens*, *Vibrio parahaemolyticus*, *Yersinia enterocolitica*, and *Corynebacterium* sp. (Lyon et al., 1993). Jenseniin G from *P. thoenii* P126, a heat stable bacteriocin, inhibits various microorganisms like *Lactobacillus delbruecki* ssp. *bulgaricus* and *Streptococcus thermophilus* (Grinstead and Barefoot, 1992) and prevents the excessive acidification of yoghurt (Weinbrenner et al., 1997). Use of purified and concentrated bacteriocins has been preferred as food additives due to more effectiveness as compared to direct application of cultures with bacteriocin producing potential due to their slow growth or production of bacteriocin in later phase of growth cycle (Faye et al., 2000).

Yoghurt was produced from raw milk by incorporating a nisin-producing strain, *Lactococcus lactis* subsp. *lactis*, along with the traditional yoghurt culture consisting of *Streptococcus salivarius* subsp. *thermophilus* and *Lactobacillus delbrueckii* subsp. *bulgaricus*. This resulted in increased storage life of the food by preventing the growth of spoilage bacteria and thus controlling the increase in acidity (Yamauchi et al., 1996). The yoghurt product can be dried, either by lyophilization or spray-drying or other means, preferably to a powder, for use in various foods (Vedamuthu, 1995). Nisin has been added to cheese spreads and other processed foods to inhibit toxin production by *Clostridium botulinum* (Taylor, 1986). Addition of nisin (12.5 ppm) in the cheese samples innoculated with 1000 spores/g showed toxicity in 16 weeks of incubation at 30°C as compared to 8 week in control. Only three toxic samples were observed in 48 weeks of incubation of samples containing 100 ppm nisin, while higher concentartion of 250 ppm prevents the toxicity in 48 weeks of incubation. However, nisin have sporostatic effect as reported by MPN data of these experiments (Taylor, 1986).

Broad spectrum acidocin CH5 (Chumchalova, 2004), acidocin 1B (Kyoung-Sick et al., 2007) and acidocin AA11 (Abo-Amer, 2007) are reported to have application in fermented products to prevent the growth of pathogenic bacteria. Acidocin B isolated from bifidobacteria has also been reported to be active against *Clostridium* sp. in fermented products like cheese or silage (Brink et al., 1994). Bacteriocins might contribute to development of flavour and quality of food products. During ripening of cheeses the starter cell culture undergo lysis to release proteinases and peptidases which contribute to flavour development in cheese (Lortal and Chapot-Chartier, 2005).

Bakery Products and Ingredients

Wheat doughs used for preparation of various bakery products may be contaminated with bacteria resulting in bread defects, including ropiness and enterotoxins production (Sorokulova et al., 2003; Smith et al., 2004). Bacteriocin at low concentration (14 AU/gm) is effective against vegetative cells of *B. subtilis*, *B. licheniformis*, *B. cereus*, and *B. pumilus* strains under experimental conditions, while its higher concentration (23 AU/gm) is required in killing of endospores (Martinez-Viedma et al., 2011).

S. aureus inhibition was also observed with addition of AS-48 in liquid caramel, pumpkin comfiture or diluted almond cream (Martinez-Viedma et al., 2009e). Bacteriocins are effective against *S. aureus*, *B. cereus*, and *L. monocytogenes* in various desserts including baker cream, soy-based desserts, and gelatin puddings (Martinez-Viedma et al., 2009d). *Listeria* contamination has been decreased by >2 log CFU per package by packaging hot dogs with cellulose based films containing 10,000 and 7,500 IU/mL nisin (Franklin et al., 2004). A gelatin form of pediocin, a class IIa bacteriocin made by lactic acid producing bacteria developed to protect hot dogs from *Listeria* contamination (Raloff, 1998).

Alcoholic Beverages

Growth of undesirable microorganisms may result in deterioration of the characteristics of alcoholic beverages. Bacteriocins are produced by food-grade lactic acid bacteria and help in preventing the development of food spoilage bacteria. In the case of wine, it offers the additional advantage of allowing a decrease of sulphurous anhydride levels in wine. Ruiz-Larrea et al. (2010) observed the effect of nisin alone and in combination with metabisulphite on red wine indicating measurable reduction of microbial population in the samples with low metabisulphite concentration combined with nisin, thereby, resulting in the preservation of wine during the ageing and storage process. A composition prepared by fortifying wort with nutritional supplement, innoculating with nisin producing culture followed by fermentation led to high shelf stability without affecting flavour and aroma of beer (Nauth, 2007).

Meat Products

L. monocytogenes is widely distributed in nature and is found in ready-to-eat meats from 0 to 50% because of its transfer from the environment to the processed food (Nesbakken et al., 1996). Bacteriocins from different lactic acid bacteria have been shown to reduce or inhibit the growth of *L. monocytogenes* in meat and meat products. Jacobsen et al. (2003) studied four different methods for using the partially purified bacteriocin or the living culture of *Lec. carnosum* 4010 as biopreservative. The living protective culture added to the sliced gas packed meat product was found to be more effective in preventing growth of *L. monocytogenes* than the use of the partially purified leucocins. Sprinkling the protective culture on the surface of meat products resulted in the highest decrease in *L. monocytogenes*. Counts of *L. monocytogenes* never exceeded 10 CFU g^{-1} during 4 weeks of storage at 10°C as compared to 107 CFU g^{-1} in control samples. Enterocin 416K1 decreased *L. monocytogenes* in Italian sausages (Sabia et al., 2003). Anti-listerial effect of bacteriocins from *L. curvatus* and *P. acidilactici* has transient effect, leading to regrowth of *Listeria* cells (Pucci et al., 1988; Benkerroum et al., 2005; Privat et al., 2008). Kouakou et al. (2010) was successfully able to delay *Listeria* rebound in artificially contaminated raw pork meat by co-inoculating the meat system with two acidifying strains *Lb. curvatus* (sakacin P) and *P. acidilactici* (pediocin AcH), thereby, improving the food safety against *Listeria*.

Novel bacteriocin compositions have been developed (Blackburn and de la Harpe, 1998) which have broad range bactericidal activity and are effective in treating and preventing various microbial infections. *Enterococcus faecium* ST5Ha isolated from smoked salmon displayed antiviral activity against human pathogen HSV1 with selectivity index of 173 (Todorov et al., 2010).

Brined Shrimp Preservation

Einarsson and Lauzon (1995) reported a comparative study to evaluate the effects of three different LAB bacteriocins i.e. nisin Z, carnocin UI49 and bavaricin A on bacterial growth and shelf-life of brined shrimp with a control having no preservatives. The shelf-life of shrimp subjected to the control treatment was found to be 10 days as compared to 16 days in crude bavaricin A (a cell-free supernatant from *Lb. bavaricus* MI 401) and 31 days with nisin Z. In control, sodium benzoate and potassium sorbate solution inhibited microbial growth during the storage period but caused decolorization and yellowing of the shrimp around the 5th week. Bacteriocin producing enterococci have been isolated from uncooked molluscs and fish for possible applications in preservation of sea foods (Valenzuela et al., 2010).

Protection of Fresh Fruit, Vegetable, and Sauces

As many of the freshly cut vegetables, fruits (Harris et al., 2003; Dupont, 2007; Doyle and Erickson, 2008), and seed sprouts (Pao et al., 2005) are consumed without cooking, this may lead to various health risk due to their contamination with pathogenic bacteria. Bacteriocins alone or in combination with chemical preservatives help in preventing the spread of pathogenic microbes. Washing of fruits with bacteriocin AS-48 inactivated the *L. monocytogenes* inoculated on fruit surface or sliced fruits (Molinos et al., 2008a). Thermostable bovicin HC5 recovered from *S. bovis* HC5 can decrease the thermal resistance spores of *Alicyclobacillus acidoterrestris*, a major spoilage bacterium in pasteurized acidic juices (de Carvalho et al., 2008). Reduction in *L. monocytogenes* cells on artificially contaminated alfalfa and soybean sprouts was also observed by keeping the material in AS-48 solution for five minutes (Molinos et al., 2005). Addition of various antimicrobials including sodium hypochlorite (100 ppm), peracetic acid (40 ppm), polyphosphoric acid (0.1–2%), or hexadecylpyridinium chloride (0.5%) with AS-48, further, increased the antimicrobial activity (Molinos et al., 2008b, 2008c). Storage period of Russian-type salad was increased by inactivation of *L. monocytogenes* or *Salmonella* strains with the action of bacteriocin AS-48 alone (Molinos et al., 2009a) or with addition of various essential oils/their bioactive components, plant extracts, and natural/synthetic antimicrobials (Molinos et al., 2009b). Fresh vegetable sauces commonly consumed in home or restaurants, if contaminated, can lead to food poisoning. AS-48 added at 80 μg/mL concentration helped in partial inactivation or complete inactivation of *S. aureus* depending on type of sauce (Grande et al., 2007).

Cyclic peptide AS-48 is produced by many enterococcal isolates (Folli et al., 2003; Franz et al., 2007). Fresh as well as processed juices are commonly spoiled by *Alicyclobacillus acidoterrestris*. Experiments showed that low concentrations of AS-48 in artificially contaminated juices (Grande et al., 2005) led to inactivation of the thermophilic sporeformer *Geobacillus stearothermophilus* in coconut milk and coconut water (Martinez-Viedma et al., 2009a) and rope-forming *Bacillus licheniformis* LMG 19409 in fresh-made apple juice and in commercial apple ciders (Grande et al., 2006). Synergic effect of AS-48 and high-intensity pulsed electricfield (HIPEF) treatment against *Lb. collinoides, Lb. diolivorans*, and *P. parvulus* was observed by Martinez-Viedma et al. (2009b).

Baby Foods

Campylobacter is one of the leading bacterial causes of foodborne illness. Use of antibiotics may lead to developing resistance that will cause sickness in human consumers. Spray-dried bacteriocin lacticin 3147 powder has effective antimicrobial activity and can be used in a range of foodstuffs like infant milk, powdered soup, yoghurt, and cottage cheese (Ross and Hill, 2004). The significance of using a bio-active powder is that it could be easily applied as a food ingredient in a variety of food items.

Bacteriocin Disinfectant

Moist disinfectant wipes or towelettes have a number of applications including the disinfection of hands, skin, food lines, and hospital surfaces, as well as applications in the dairy and food processing industry. The bacteriocin molecules, which are stable to drying, water rinsing, freezing, and have long stability profile, are attached to the surface or article which can later on interact with susceptible bacteria deposited on the treated surface and kill the microorganisms (Blackburn and de la Harpe, 1998). These detached bacteriocin molecules may also kill susceptible bacteria present on foods or other substances in contact (Daeschel and McGuire, 1995).

Aquaculture

Pathogenic bacteria are found to be the causative agents of bad quality of water, stress, and diseases. Due to the high consumption of antibiotics in aquaculture and its undesirable affects, scientists initiated a search for alternative methods of disease control and growth promotion. Vijayabaskar and Somasundaram (2008) isolated *Bacillus* sp. and used them as a probiotic in fresh water fish Tilapia (*Oreochromis mossambicus*) against the most common fish pathogen *Aeromonas hydrophila*. Higher antagonistic activity was recorded from bacteriocin compared to the intracellular protein against *A. hydrophila*. After feeding with the potential probiotics for 25 days, challenge by pathogen indicated reduction in disease caused by *A. hydrophila* in fish. Tilapia exhibited significant difference in growth and survival between probiotic and control groups. The use of *Lactobacillus* also enhances the production rate of rotifers, which act as biocarriers of probiotics.

Livestock

Bacteriocin is also reported to play an important role in controlling the over growth of potentially pathogenic bacteria in animal feedstock. Lack of maternal bacterial flora or noninduction of proper immune system in newly hatched broiler chicks, makes them prone to infection. Application of the bacteriocin-producing *E. faecium* after hatching increased the survival rate of young broiler chicks infected with the poultry pathogen *S. pullorum* (Audisio et al., 2000). Microcins produced by *E. coli* helped in killing of *S. typhimurium* in adult chickens (Gillor et al., 2004). Enterocin A has shown antagonistic effect to *S. dusseldorf* in gnotobiotic Japanese quails (Laukova et al., 2003). The addition of the recombinant probiont to the drinking water significantly reduced the abundance of *S. typhimurium* in chickens (Wooley and Shotts, 2000). *Enterococcus* bacteriocin has also displayed their potential for possible application as probiotics adjunct for poultry (Strompfova and Laukova, 2007).

There have been reports that administration of colicin-producing bacteria into the rumen of cows reduces enteric pathogens in the animal (Diez-Gonzalez, 2007). A probiotic mixture Bovamine^{TM} of *Lb. acidophilus* and *Propionibacterium freudenreichii* also reduced levels of *E. coli* O157:H7 colonization in cattle. An antilisterial bacteriocin salivaricin P from *Lb. salivarius* DPC6005 is highly active against lactic acid bacteria, including lactobacilli and *Enterococcus* sp. (Barrett et al., 2007) and helps to out-compete the resident gut microbial communities and colonize the ileum better than the other *Lactobacillus* strains (Walsh et al., 2008). Sorbic acid and live (secreting bacteriocin) or dead microorganisms (containing bacteriocins) or bacteriocin (encapsulated/carrier bounded) was used in feed-stuffs or in a mixture with other feed additives for improving the hygienic status of the feed and for improving performance in agricultural livestock rearing (Raczek, 2004).

Campylobacter also causes infection in poultry and lead to foodborne illness. Further development of resistance to antibiotics adds to problem. Scientists at University of Arkansas applied the bacteriocins which decreased the infecting bacteria and also changed the environment conditions prevailing in gut, thus, decreases the chances of development of bacteria. Administration of bacteriocin before processing removed even the undetectable levels of the pathogen, thereby, decresing the risk for human health. Bacteriocins seemed to decrease the mucin secretion (energy source for pathogen) by decreasing the goblet cells in bird's intestine (Donoghue, 2007).

Clinical Applications

Bacteriocin mutacins produced by *Streptococcus mutans* VSM43 isolated from human clinical oral cavity inhibit the growth of other mutans streptococci, many other gram-positives and some gram-negative bacteria and may be a parallel candidate for use against dental caries (Ahmad and Rasool, 2003). Bacteriocin produced by strains of lactic acid bacteria are used in the production of OMX toothpaste that inhibits oral pathogenic bacteria, thereby, protecting gum infections, tooth decay, gingivitis (Howell et al., 1993; McConville and Beecham, 1995) and improve oral hygiene (http://www.hiwtc.com/buy/probiotic-toothpaste-49313/). A method for preventing or suppressing the fermentation of sugars by oral bacteria by salivary enzymes by action of a lathionine-containing bacteriocin was reported (Blackburn and Goldstein, 1997). This bacteriocin can be incorporated into a mouth-rinse, spray, gum, or lozenge or other formulations prepared for application following consumption of sugar and complex carbohydrate containing foods, confectioneries, and beverages. Tooth enamel softening and tooth decay, are major problems observed by consumption of sport and energy drinks having low pH and high acidic contents. Addition of AS-48 inactivated *L. monocytogenes*, *B. cereus, B. licheniformis*, and *S. aureus,* thus, making it a good candidate as a natural preservative (Martinez-Viedma et al., 2009c).

Bacteriocin of LAB also has their applications in medical and personal care (Dicks et al., 2011). Bacteriocin epidermin and gallidermin produced by *Staphylococcus epidermidis* and *S. gallinarum*, respectively, has been reported to effectively treat the skin infection (Kellner et al., 1988). Lacticin 3147 having excellent activity over a broad pH range, absence of cytotoxicity towards eukaryotic cells, broad spectrum of activity at nanomolar concentrations, inhibit systemic *S. aureus* infection in mice, thereby, making it a promising candidate for potential applications in human medicine (Piper et al., 2012). Bower et al. (2002) reported the application of nisin coating on Teflon FEP intravenous cathters and PVC tracheotomy tubes prevented the growth of *S. ureus, S. epidermidis*, and *S. faecalis*. Anti-campylobacter bacteriocin purified from *Lb. salivarius* SMXD51 isolated from chicken ceca helped in controlling the Human campylobacteriosis (Messaoudi et al., 2012).

Bacteriocin and Toxicity

Colon of healthy adults harbor about 300–400 cultivable species, belonging to more than 190 genera, predominantly *Bacteroides, Eubacterium, Bifidobacterium, Peptostreptococcus, Enterobacteriaceae, Streptococci*, and *Lactobacilli* (Gedek, 1993). Lactic acid bacteria have wide applications especially in food-processing and medical industry. Lactic acid bacteria are commonly used in animal or human nutrition as probiotics. Studies have suggested that bacteriocin do not have any toxicity for humans and animals or any accumulation in the organisms as these are degraded by proteases into nontoxic amino acids. The effect of nisin, nisin-producing *Lactococcus lactis* strain CHCC5826, and the nonnisin-producing *L. lactis* strain CHCH2862 on composition of the intestinal microbiota of human flora-associated rats was studied (Bernbom et al., 2006). Significantly, increased number of *Bifidobacterium* cells in fecal samples decreased the number of enterococci/streptococci due to the presence of both the nisin-producing and the nonnisin-producing *L. lactis* strains. The toxicity studies and its long history of use suggest that nisin can be used safely (http://www.efsa.eu.int/science/afc/afc_opinions/catindex_en.html), however, low cytotoxicity of nisin toward epithelial cell lines HT29 and Caco-2 was observed (Maher and Mcclean, 2006). Cytotoxicity of pediocin PA-1 have been reported in studies against simian virus 40 transfected human colon cells and Vero monkey kidney cells (Murinda et al., 2003). Carnobacteriocins Cbn BM1 and Cbn B2, from *Carnobacterium maltaromaticum* CP5, separately or in combination showed antimicrobial activity against *Listeria* sp., *Enterococcus* sp. and *Carnobacterium* sp. Two peptides alone or in combination, at concentration 100-fold higher than those required for antimicrobial activity, were not cytotoxic for human colon adenocarcinoma Caco-2 cell lines; thus might find application as potential biopreservatives to prevent a growth of microbes especially *Listeria* sp. Existence of a synergistic mode of action between Cbn BM1 and Cbn B2 permit to use very low levels of each bacteriocin (Jasniewskia et al., 2009).

Miscellaneous Applications

Bacteriocin found their applications in sewage water and manure decontamination on large-scale breeding farms (Laukova et al., 2000). Bacteriocins produced by bacteria present in complex microbial community in rumen plays an important role in regulation of rumen microbial ecosystem (McAllister et al., 2011). *Butyrivibrio fibrisolvens* OR79 produced butyrivibriocin OR79A and *B. fibrisolvens*AR10 produced butyrivibriocin AR10 are class I (lantibiotic) and class II (nonlantibiotic) bacteriocin respectively (Kalmokoff et al., 1999; (Kalmokoff et al., 2003). Studies have shown that these bacteriocins may be as useful in limiting methane production and amino acid degradation in the rumen (Lema et al., 2001; Pattnaik et al., 2001; Lee et al., 2002). Nisin- and pediocin-producing lactic acid bacteria have been shown to reduce intestinal colonization of pathogenic enterococci (Millette et al., 2008). Probiotic *E. coli* strain Nissle 1917 produces microcins H47 and M and has been shown to reduce neonatal diarrhea in calves (Buenau et al., 2005; Patzer et al., 2003). Cariogenic diet containing *S. mutans* C3603S bacteriocin fed to pathogen-free rats infected with *Streptococcus mutans* PS-14 serotype C showed fewer carious lesions as compared to control and had 58.7% caries-inhibitory effect (Ikeda et al., 1985).

The spermicidal activity of two bacteriocins, lacticin 3147 and subtilosin A, on bovine, horse, boar, and rat sperm makes them extremely attractive agents to prevent unwanted pregnancy but also helps them to combat the growing prevalence of sexually transmitted infections (Silkin et al., 2007). Recombinant strains of *Lactococcus lactis* and bacteriocin UL4 have the potential as a promising vaccine to prevent the infection of fishes by *Aeromonas hydrophila* and thereby reducing the excessive use of antibiotics in controlling diseases and for the overall improvement of the health of fish (Karunakaramoorthy, 2009). Research on using nonpathogenic strains of *Enterococcus faecalis* that produce bacteriocin has been carried out to inoculate the noses of children, so as to protect them from getting pneumococcal pneumonia. Similarly, bacteriocins derived from *E. faecalis* SL-5 can inhibit growth of *Propionibacterium acnes* by having antibacterial activity against them and preventing, treating, and improving acne (Chung and Seo, 2010). Transgenic potato developed for expressing the synthetic derivative MsrA2 (*N*-Met-dermaseptin B1) of antimicrobial peptide Dermaseptin B1 and N terminal modification of temporin A (MsrA3), have broad spectrum resistance from various phytopathogens and extended the storage life of tubers (Osusky et al., 2004, 2005). Bacteriocin-producing avirulent mutants helped in controlling a phytopathogenic *E. carotovora* subsp. *carotovora* responsible for the causing diseases in a number of important food crops (Perombelon and Kelman, 1980; Kikumoto and Takahar, 1993).

Although several reports describe the detection, isolation, and biochemical characterization of bacteriocins (El-Shafie et al., 2008) and their potential use as natural preservatives, but the functionality of these strains under industrial food processing conditions is still questioned. However, there is substantial reluctance by the industry in developing commercial bacteriocin preparations because of the costly production and difficulties in food grade approval.

COMMERCIALLY AVAILABLE BACTERIOCINS

For the use of biopreservative on commercial scale, it has to fulfill certain requirements of being nontoxic, stable, should not affect the organoleptic properties of the food products, economical, accepted by recognized authorities, and used in low concentration (Holo et al., 2002). Although many other type of bacteriocin such as subtilin, cerein, thuricin, plantaricin etc. (Aunpad and Na-Bangchang, 2007) have been isolated and characterized from different bacteriocin producing strains of bacteria (Corr et al., 2007; Lee et al., 2007; Riazi et al., 2009), yet, till date only commercially produced bacteriocins are Nisin (*Lactococcus lactis*) and Pediocin (*Pediococcus acidilactici*) and others are still in a process of getting commercial status to be used as food preservatives (Table 3). Nisin, having broad spectrum of antimicrobial activity, has only been given the GRAS status biopreservatives by Food and Drug Administration and is extremely effective in a number of food systems including canned foods

Table 3 Commercially produced bacteriocins

Sr No.	Bacteriocin	Commercial name	Producer Strain	Manufacture
1.	Nisin	Nisaplin	*Lactococcus lactis*	Danisco, Copenhagen Denmark
2.	Pediocin PA1	ALTA 2431	*Pediococcus acidilactici*	Kerry Biosciences Carrigaline Ireland
3	Nisin	MAYNISIN	Lactococcus sp.	MAYSA GIDA San ve Tic. A.S Turkey
4	Nisin	Nisitrol	Lactococcus sp.	Bimal Pharma Pvt. Ltd. India
5	Nisin	SAFRESH™	Lactococcus sp.	Wuhan Amth Biotechnology Co., Ltd.China
6	Nisin	YP-1000 Nisin	*Lactococcus lactis*	China (National) Abrasives Corp

and dairy products to prevent food spoilage and increase shelf life (Chen and Hoover, 2003). Nisin inhibits virtually all gram-positive bacteria in food.

CONCLUSIONS

Bacteriocins possess vast potential as additive or as substitute for existing antimicrobial compounds, which can be used in formulation of different food products. Isolation of novel bacteriocins, bacteriocin modifications with protein engineering, construction of food grade vectors, regulation and expression of heterologous proteins, and modification are the areas of research. In addition, new applications of bacteriocins are coming up in the areas of food processing, livestock and pharmaceutical industry. Extensive research is still needed to discover more bacteriocins, which are commercially viable and have GRAS status.

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