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Marine bacteriocins and their potential application for seafood preservation

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Abstract- *Seafood is highly perishable, presenting a rapid loss of its quality soon after capture. Temperature is the critical parameter that impacts on seafood shelf-life reduction, allowing the growth of foodborne pathogens and spoilage microorganisms. In recent years, the search by additional methods of preserving seafood has increased, able to ensure quality and safety. Several natural preservatives have highlighted and gained considerable attention from the scientific community, consumers, industry, and health sectors as a method with broad action antimicrobial and generally economical. Natural preservatives, from different sources, have been widely studied, such as chitosan from animal sources, essential oils, and plant extracts from a plant source, lactic acid bacteria, and bacteriocins from microbiological sources and organic acid from different sources, all with great potential for use in seafood systems. The ocean supports a rich biodiversity, of which bacteria comprise a vast number. Exploration of the ocean for novel bacteriocins is built on the idea that because marine habitat is an extreme environment, highly competitive marine bacteria could produce more potent bacteriocins as compared to compounds isolated from other sources. This review provides updated information about the production, mode of action and applications of marine bacteriocins in seafood preservation. In addition, the actual and potential applications of marine bacteria and their bacteriocins in aquaculture and briefly on the potential uses in other fields have been discussed. Moreover, literature data from isolation, biochemical characterization, and antimicrobial assay reports have also been integrated to provide a contemporary understanding of marine bacteriocin potentials.*

Keywords :*antimicrobial, marine bacteriocins, shelf-life, seafood, probiotics, aquaculture.*

I. INTRODUCTION

Seafood, including various species of fish, crustaceans, mollusks, and echinoderms, are excellent sources of protein, fat, vitamins, and minerals and are popular due to their delicacy with high nutritive value. However, the shelf-life of seafood is limited because of the high contents of various nutrients, neutral pH, and high moisture content [1]. The rapid microbial and biochemical reactions that occur in seafood immediately after death lead to changes in sensory and nutritional properties that reduce the shelf-life [2]. Generally, seafood is abundant in polyunsaturated fatty acids (PUFAs), which make it more prone to lipid oxidation. Formation of unpalatable odor and flavor, loss of nutrition, production of unhealthy molecules, and color changes are mainly the consequences of lipid oxidation in seafood [3].

Microbiological, chemical, and physical changes contribute to the complexity of seafood spoilage. The initial loss of fish freshness is attributed to indigenous enzymes and chemical reactions, whereas complete spoilage in fish is a function of microbial metabolic activities [4]. The distance between the harvesting or capturing ground and processing facilities, storage temperature, and processing methods are essential in determining the quality and deterioration of seafood. Extrinsic and intrinsic factors and capturing methods can positively or negativelyimpactthe quality and shelf-life of seafood [5]. During the processing, distribution, and storage of seafood, hazard analysis of critical control point, good hygienic practices, and good manufacturing practices are crucial for controlling the spoilage [6]. Extensionof the shelf-life of food products, using diverse preservationtechniquesandnonthermal technologies has gained an increasing interest

because of high demand for fresh chilled foods, especially primequality seafood [2, 7]. Prevention of nutritional and sensory losses caused by microbiological, enzymatic, or chemical changes,andshelf-life extension of food are usually achieved by chemical preservatives, such as sodium benzoates, sodium nitrite, and sulfur dioxide. Nonetheless, accumulation of these synthetic preservatives in tissues can be detrimental to health [8]. Treatment with salt is one of the common and oldest natural preservative methods used widely for shelf-life extension of seafood because of its low cost, as well as simplicity [9].The effectiveness of salt as a preservative is solely due to its ability to reduce the water activity in the seafood muscle, thereby inhibiting the growth of bacteria and enzymatic activity. Halotolerant and halophilic bacteria grow in saltpreserved seafood, by using energy to exclude salt from their cells, thus avoiding protein aggregation (salting-out) in their cytoplasm [10]. Uncontrolled growth of these organisms can also lead to spoilage by fermentation. Nevertheless, salting of seafood can affect the taste and provides a high sodium content in products [11].

In recent years, researchers have put much effort into searching natural preservatives that couldinhibit the growth of bacteria and fungi in food. Meanwhile, a growing number of consumers areaware of the potential negative health effects of chemical preservatives, which has prompted thefood industry to find natural products used and developed as alternatives. Natural preservativesare available from a variety of sources including plants, animals, bacteria, algae, and fungi [12,13].Microbial derived preservatives (e.g., bacteriocin), plant derived preservatives (thyme essential oil,tea polyphenols, rosemary extract, etc.), and animal derived preservatives (e.g., chitosan from crab orshrimp shells) have been demonstrated to have antimicrobial or antioxidant properties. In addition,antimicrobial compounds produced by bacteria, algae and fungal (mushroom) could be served as potentialsources of new antimicrobial substances for use as natural preservatives in food.

Bacteriocins are found in almost every bacterial species examined to date, and within a species tens or even hundreds of different kinds of bacteriocins are produced.Although a huge number of marine bacteria and bacteria producing bacteriocin-like compounds have been investigated with remarkable therapeutic potential application of marine bacteria and bacteriocins derived from them may have remarkable potential in aquaculture systems.

The aims of this review were to provide updated information about the production, mode of action and applications of marine bacteriocins in seafood preservation. In addition, the actual and potential applications of marine bacteria and their bacteriocins in aquaculture and briefly on the potential uses in other fields have been discussed. Moreover, literature data from isolation, biochemical characterization, and antimicrobial assay reports have also been integrated to provide a contemporary understanding of marine bacteriocin potentials.

2. Seafood Spoilage

Any change in the initial condition of seafood that results in an unpalatable odor, taste, appearance, and texture is referred to as spoilage. This change can beattributed to enzymatic, chemical, or microbial activities in the seafood [14]. [15] reported that rigor mortis, which is a biochemical change in fish muscle that occurs immediately after death, led to the loss of muscle flexibility. Activities of indigenous proteases and lipases, spoilage organisms, and lipid oxidation have been reported to be responsible for spoilage or deterioration during post-rigor mortis storage [14,16].Chemical, microbial, and enzymatic spoilage in seafood can be controlled by

pretreatment, preservatives, and packaging in which the sensory and nutritional properties of the product can be maintained.

Microbial spoilage in seafood. Seafood is highly vulnerable to invasion by opportunistic and pathogenic microorganisms. Habitat, which is a microbe-richenvironment, mostly determines the microbial load of seafood[14,17]. Generally, spoilagein seafood is mainly caused by the growth and metabolismof microorganisms associated with the production of biogenicamines, alcohols, histamine, putrescine, sulfides, organic acids,aldehydes, and ketones [17]. Psychrophilic bacteriaare the main group of microorganisms responsible for spoilagein chilled or refrigerated seafood. [18] identified aerobic or facultative anaerobic psychrotrophicGram-negative bacteria, such as *Moraxella*, *Shewanella putrefaciens*,*Acinetobacter*, *Pseudomonas*, *Photobacterium*, *Aeromonas*, *Flavobacterium*,and *Vibrio*, as major spoilage organisms in seafood. Specificspoilage organisms such as *Shewanella*, *Photobacterium phosphoreum*,and *Pseudomonas* are considered the major causes of seafoodspoilage [19].Gram-negative bacteria are the major contributors to spoilagein seafood. However, continuous processing or extended storage/transportation provides opportunities for Gram-positivebacteria to also dominate and cause spoilage [20]. [21] reported bothGram-negative bacteria (*P. phosphoreum*) and lactic acid bacteria(LAB) as the major spoilage bacteria in fish. Gram-positive bacteria,such as *Micrococcus*, *Corynebacterium*, *Bacillus*, *Staphylococcus*,*Clostridium*,*Streptococcus*[20]and *Brochothrixthermosphacta*[22,23]were also identified as spoilagemicro- organismsin seafood. It could, therefore, bededuced that both Gram-negativeand Gram-positive bacteria are responsible for the spoilageof seafood. However, the sampling location, geographic location,andmethod of fishing are factors determining the type and numberof microorganisms [14]. The low-molecularweightsubstances, such as small peptides, carbohydrates, andfree amino acids in the tissue, are utilized by microorganismsas an energy source for growth and production of several byproducts,including biogenic amines [24], histamine [25], sulfur-containingcompounds [26], and other components.The enzymatic activity of some other bacteria, such aspsychrotolerant *Enterobacteria*,*Vibrio* spp, *Aeromonas* spp, and*S. putrefaciens* have been reported to reduce trimethylamineoxide (TMAO) in seafood to trimethylamine (TMA), whichis responsible for the fishy odor [27,28]. TMA productionis accompanied by the development ofhypoxanthine, which causes a bitter taste in seafood [29]. Production of hypoxanthine is induced by indigenousenzymes or, relatively more quickly, by bacteria via decompositionof nucleotides (inosine or inosine monophosphate [24,25].

Chemical deterioration in seafood. In general, seafood is rich in lipids, especially fats containinglong-chain PUFAs [30]. Lipids playa major role in off-flavor and off-odor development and loss inthe nutritional value of seafood [31]. Depletion of fat-soluble vitamins and other compounds is alsoa consequence of lipid oxidation [32,33]. Lipid oxidation involves several stages. The mechanisms oflipid oxidation areillustratedin Figure 1. An abstracted labilehydrogen atom from a fatty acyl chain can initiate lipid oxidation,with free radical production. Metals, ions, irradiation, and heatare catalysts for the free-radical formation. Free radicals reactexpeditiously with oxygen to form theperoxyl radical, which canfurther abstract a hydrogen atom from another fatty acyl chain,thereby producing a new free radical and hydroperoxide. Thenew free radical can then continue the chain reaction [34,35].Lipid oxidation is terminated when there is a build-up of freeradicals with the formation of non-radical

products [36]. The rate of oxidation isgoverned by oxygen availability,light, the presence of metals, and moisture, temperature, anddegree of unsaturation of the lipid [37].Nevertheless, primary products, mainly hydroperoxides, are notstable. Secondary products of lipid oxidation are formed as aresult of decomposition of primary products. Thus, both primary(free fatty acids [FFAs], dienes, and peroxides) and secondary(aldehydes, trienes, and carbonyls) products are generated fromthe lipid oxidation process. Overall, the amounts and types ofoxidation products depend on the extent of the oxidation reactionand fatty acid composition [38]. [31] noted that pre-slaughteractivities (physical injuries and stress), post-slaughter activities(cold shortening and tenderization techniques, temperature, andpH), and processing parameters (raw materials quality, processingtemperature, size reduction, additives, type of packaging, anddistribution and storage conditions), were factors influencing theintensity and rate of oxidation.Lipid oxidation can be induced by several prooxidants(hemoglobin, myoglobin, and cytochrome c) [14].Deoxygenated or oxidized hemoglobin, which are prooxidantsmostly found in the blood of fish, are responsible for acceleratedlipid oxidation ([39].Bleeding could lower lipid oxidation, associated with thedecreased prooxidant present in the blood [3,37]. Apart from theoff-flavor development in seafood, loss of functionality, as a resultof protein oxidation, occurs when secondary oxidation productsreact with proteins, amines, and peptides [40.Denaturation of myofibrillar and sarcoplasmic proteins is also aresult of interaction between those proteins and FFAs formedduring hydrolysis of lipids ([41].

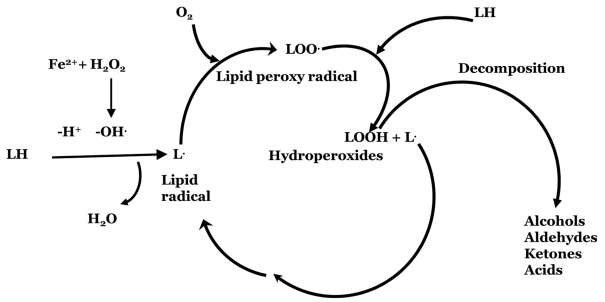

Figure 1. Mechanism of lipid oxidation in seafood. LH stands for fatty acid.

Enzymatic deterioration in seafood. The process of degrading proteins by indigenous enzymes,known as autolysis, starts immediately after the completion of rigormortis. This process creates a favorable environment for bacterialgrowth [14]. Alteration in the sensory propertiesof seafood can be attributed to proteases and lipases [42]. Even during refrigeration and frozen storage, autolysisoccurs in seafood at a very slow rate ([43]. However,during improper storage, protein is rapidly degraded, via a processmediated by indigenous and microbial proteases. [44] Chymotrypsin,cathepsins, trypsin, lipase, and phospholipase are reportedly foundin the hepatopancreas, spleen, and pyloric ceca of seafood, whereaspepsin is located in the stomach [44].Belly burst, which commonly occurs in fish, is a function of theenzymes in the fish gut, causing rapid protein decomposition.Textural changes (meat toughening) along with the production offormaldehyde, during the storage and processing of seafood, arealso results of enzyme activities [14]. Trimethylamineoxide demethylase, found in some fish, induces the formationof formaldehyde by demethylation of TMAO to dimethylamine(DMA) and formaldehyde [45,46].Formaldehyde cross-links proteins via methylene bridging, whichmakes fish muscle tough and with low water-holding capacity[47]. Melanosis (black pigment formation)in shrimp is also a result of tyrosinase or polyphenol oxidasepresent in the shrimps [48].The products of proteolysis (free amino acids and peptides) canserve as the nutrients for microbial growth, leading to spoilage,in conjunction with the formation of biogenic amines [14,49]. Temperature and pH are factorsaffecting protease activity. Optimum pH values for most proteasesare within alkaline and neutral range [14]. Thereduction of TMAO to

TMA and other basic volatiles by theaction and metabolism of the endogenous or microbial enzymesincreases the pH of stored seafood [46,50]. Fat in seafood can also be hydrolyzed by lipase or phospholipase [51,52]. FFAs liberated in seafood can readily undergooxidation, which contributes to the formation of off-odor,particularly fishy odor. The fishy odor is related to aldehydes,mainly polyunsaturated aldehydes [53]. Thefishy odor intensity in fish with bleeding was lower than that ofunbled fish [53]. Additionally, lipoxygenaselocated mainly in gill or skin can induce oxidation in storedfish, particularly when the fish is stored for an extended time [54].

3. Microbial risk in seafood

Microbial pathogens in seafood. Microbial seafood pathogens can be classified in two categories a) Indigenous bacteria that are naturally present in the marine environment i.e. *Vibrio vulnificus,V. parahaemolyticus* and *V. cholerae,Listeria monocytogenes ,Clostridium botulinum* and *Aeromonas hydrophila*. The presenceof indigenous microorganisms is normally not a safety concern since they are present at toolow level to cause disease. Moreover, adequate cooking eliminates those bacteria or their toxin (toxin of *C. botulinum* is thermolabile). Therefore, the hazard concerns products in whichthe growth of those bacteria is possible during the storage period and which are eaten rawor insufficiently cooked. It can be the case for *Vibrio* in raw fish or tropical shrimp preparation. *Vibrio* are mesophilic bacteria found in tropical water or in temperate water at the endof summer. Their growth is very rapid if the products are kept some hours at room temperature. *L. monocytogenes* is also a problem in lightly preserved fish products (LPFP) such as cold smoked, lightly marinated fish or insufficiently cooked seafood stored under VP or MAP. During the extending shelf-life of those products,*L. monocytogenes* can still develop and reach unacceptable concentration. Insufficiently salted seafood stored in anaerobic condition or traditional fermented fish can also support growth of *C. botulinum* and production of the botulinic toxin. Scombroid and Clupeid fish kept some hours at abuse temperature (> 5°C) with high histamine content. The origin of histamine producing bacteria is not completelywell established although there is evidence that some of them are present in the gut, gills and skin of the fish. Most of the histamine producers are mesophilic bacteria (*Morganella morganii, Hafnia alvei, Raoultella planticola*) that produce histamine when fish is stored at abuse temperature, for instance during storage on the vessels or during the thawing step before processing. More recently, psychrotolerant bacteria (*Photobacterium phosphoreum, Morganella psychrotolerans*) that grow at 2°C have been associated with histamine fish poisoning in cold-smoked tuna (Emborg and Dalgaard, 2006). Once produced, histamine is not destroyed during the canning process and may cause serious problem in those products. All those indigeneous bacteria can also post contaminate products during the processing step, either by cross-contamination in industry or because some of them (*L. monocytogenes*) are ubiquitous bacteria naturally present in many food industrial environments or in human skin.b)-Exogenous bacteria due to post contamination during fish processing: those bacteria are the same as those that can be found in other food products i.e. *Staphylococcus aureus, Salmonella, Shigella, Clostridium perfringens, Bacillus cereus, Yersinia enterocolitica* or enterohaemorrhagic *Escherichia coli.* Some of those bacteria can also be present in costal and estuarine marine water or in aquaculture ponds, due to human activities. They constitute a serious problem since low dose can cause illness. Normal cooking eliminates the risk but a lot of ready-to-eat food are not or insufficiently cooked (shellfish salads, shrimps, soup etc.). Moreover, the toxin of *S. aureus* is heat stable. The different

pathogenic bacteria, symptoms, minimal infectious doses and seafood responsible for infection are summarized by [55,56].

Microbial seafood safety risk assessment. Different qualitative and quantitative risk assessment strategies have been used tocategorize risk from seafood.Risk categories and associated microorganisms are describedin Table 1.In a semi quantitative seafood safety risk assessment performed on statistics ofseafood-borne illnesses during the period 1990–2000 in Australia, Sumner and Ross (2002) [57] have shown that very high risks were due to*V. parahaemolyticus* and *V. cholerae* in cookedprawns, *V. vulnificus* in oysters,*L. monocytogenes* in cold-smoked seafoods,enteric bacteriain imported cooked shrimpeaten by vulnerable consumers and scombrotoxicosis. Almost allthe hazard/product pairs in this category have caused the outbreaks of food poisoning inAustralia. In developed countries, changing in consumers habit has led to an increase ofready-to-eat and convenient food, concept that includes both the easy-to-use aspect and anextended shelf-life of the products. The nutritional aspects are also more and more taken intoconsideration by the consumers who want natural products, with technological treatment andlevel of preservatives as low as possible. LPFP, like carpaccio-type marinated fish, coldsmokedfish, peeled and lightly cooked shrimp, desalted cod packed under VP or MAP etc.,meet those requirements and their production has increased dramatically those last years.The major safety risk associated with LPFP is*L. monocytogenes* with a prevalence quiteelevated, varying from2 to 60% depending of the studies [57- 62]. *L. monocytogenes* may be present in raw material in low numberbut contamination mainly occurs during processing. A strict hygienic manufacturing practicehas been emphasised to reduce the cross contamination with *L. monocytogenes* with dailycleaning and disinfection of the production lines and special attention to hygiene of theemployees. However, a production of LPFP consistently free of the bacterium seemsimpossible as *L. monocytogenes* is not destroyed by the different processing steps. The riskassociated with consumption of LPFP is due to the possible growth of *L. monocytogenes*rather than to the initial contamination of freshly processed products, which are commonlyinferior to 1 CFU g-1. *L. monocytogenes* can multiply at low temperatures, in a wide range ofpH, in aero and anaerobic conditions in the presence of salt or smoke and it can sometimesoverpass the European tolerated limit of 100 CFU g-1 (Commission Regulation1441/2007/EC) [63].In those kind of products with an extended shelf-life, psychrotrophic LAB have time todevelop, therefore, their use as protective culture to prevent *L. monocytogenes* and spoilingmicroorganisms is a subject of increasing investigations.

Table 1Risk categories for seafood products and associated microorganisms

Risk	Seafood products	Agent
High	Mollusc (fresh or frozen)	Virus, bacteria, toxin from microalgae (heatstable)
	Raw fish : Ceviche, Suchi etc.	Indigenous bacteria (*Vibrio*)
	Lightly preserved fish (NaCl < 6% WP, pH > 5): carpaccio, coldsmoked fish, marinated products, gravads etc.	Growth of indigenous bacteria(*Listeria monocytogenes*, productionof toxin from *Clostridium botulinum*)
	Mildly heat processed: cooked and peeled shrimp, salads, soup etc.	Recontamination with enteric bacteria, growth of *Listeria monocytogenes*, *Vibrio*

	Scombroid fish	Histamine production
Low	Cooked fish and crustacean	Ciguatera in tropical area
	Semi preserved fish (NaCl > 6% WP, pH < 5): salted, dried, marinated, hot smoked fish etc.	Recontamination with enteric bacteria
	Heat processed: sterilised, canned etc.	*Clostridium botulinum* spore

4. Bacteriocin basics

Like all organisms in nature, bacteria too have their own immune system and defense mechanisms. The antagonistic factors like antibiotics, bacteriocins, lysozymes, siderophores, proteases, and/or hydrogen peroxide and the alteration of pH values by organic acids produced either singly or in combination act as defense substances. Bacteriocins are potent antimicrobial peptides and proteins, found in almost every bacterial species examined till date, and within a species tens or even hundreds of different kinds of bacteriocins are produced [64]. The three types of cells in a microbial community are, bacteriocinogenic(producebacteriocin), sensitive, or resistant to each bacteriocin. Thus in marine environments, all three cell types compete with each other for limited resources, with only a small percentage of bacteriocinogenic cells induced to produce and release bacteriocin. While some sensitive cells are killed immediately by the bacteriocin, others harbor mutations that impart resistance. These resistant cells rapidly displace the producer cells. In contrast to traditional antibiotics that are used in human health applications, bacteriocins mostly target members of the producer species and their closest relatives [65]. Hence they are classically considered to be narrow spectrum antibiotics. Halobacteria and archaea too produce their own version of bacteriocins, the halocins [66].Some bacteriocins are capable of inhibiting archaea, [67]but there is no confirmed inhibition of bacteria by a halocin, although there are reports that halophilic archaea are capable of inhibiting halophilic bacteria. Bacteriocin was first discovered by Gratia in 1925, [68]during his search for ways to kill bacteria. He named it a colicine because it killed *E. coli*. The term bacteriocin was coined by Jacob and coworkers in 1953,[69] which paved the way for the development of microbial antibiotics and the discovery of bacteriophages, all within the span of a few years. High-through put sequencing technologies reveal that bacterial diversity is larger than expected in marine microbial ecology and contains an extremely large number of microbial genes of unknown function [70]. Nevertheless, only a few bacteriocins and bacteriocin- like- substances have been described from marine bacteria. In the limited knowledge of marine bacterial biodiversity and the urgent requirement for antibiotic alternatives, the marine bacteriocin research is an open alternative in the near future.

Bacteriocin definition. Bacteriocins are ribosomally synthesized proteinaceous compounds, lethal to closely related species of producing bacteria, the latter being protected by self immunity. These toxins play a critical role in mediating microbial population or community interactions. Bacteriocins may serve as anti-competitors enabling the invasion of a strain into an established microbial community or act as communication molecules in bacterial consortia like biofilms. i.e., they play a defensive role and act to prohibit the invasion of other strains or species into an occupied niche or limit the advance of neighboring cells [71]. An additional role proposed by Miller & Bassler [72] for Gram-positive bacteriocins is in quorum sensing. Some bacterial species produce

toxins which exhibit numerous bacteriocin-like features, but they are yet not fully characterized; such toxins are referred to as bacteriocin-like inhibitory substances, or BLIS. This review focuses on bacteriocins [73-77] and bacteriocin like substances [78-81] isolated from marine environment and marine food products [82,83]. A precise definition of the bacteriocins is obscure and futile. Conventional criteria for definition of bacteriocins were based on the characteristics of colicins. These criteria have been used in varying combinations and applied with different degrees of consistency and proof in defining other bacteriocins: (i) A narrow inhibitory spectrum of activity centered about the homologous species; (ii)a bactericidal mode of action; (iii) the presence of an essential, biologically active protein moiety; (iv) attachment to specific cell receptors;(v) plasmid-borne genetic determinants of bacteriocin production and of host cell bacteriocin immunity; (vi) production by lethal biosynthesis (i.e., commitment of the bacterium to produce a bacteriocin will ultimately lead to cell death) [84].The marine environment differs substantially from terrestrial and fresh water habitats because of its exigent, competitive and aggressive nature. The estimated density of bacteria in seawater and sediment ranges from 10^5 to 10^7/mL and 10^8 -10^{10}/g respectively [85]. Little is known about the diversity of marine microorganisms. The number of species of microorganisms has been estimated from as low as 10^4 -10^5 to as high as 10^6 –10^7 [70]. Bacteriocins produced by marine bacteria are primarily of interest to researchers due to their potential as probiotics and antibiotics in the seafood industry and marine aquaculture [85,86]. The first marine bacteriocin was isolated from *Vibrio harveyi* (formerly *Beneckea harveyi*) by McCall & Sizemore [89] when they screened 795 strains of *Vibrio* spp. isolated from Galveston Island, Texas. The identification of harveyicin led to numerous bacteriocin-screening studies in marine bacteria, which focused on biochemical characterization of bacteriocins and BLIS.

A study by Wilson et al., [90]on surface-attached bacteria isolated from Sydney Harbor, Australia, revealed that approximately 10% of surface-attached marine bacteria possess antibacterial activity. Proteinase K treatment attributed this inhibitory activity to proteinaceous substances such as bacteriocins or BLIS. Antimicrobial screening of 258 bacterial strains from water and sediment in the Yucatan peninsula revealed 46 strains of genera *Aeromonas*, *Burkholderia*, *Photobacterium*, *Bacillus*, *Pseudomonas*, *Serratia* and *Stenotrophomonas* with antimicrobial activity. Around fifty percent of this antimicrobial activity was attributed to bacteriocins or BLIS [91]. A thermostable bacteriocin BL8 from *Bacillus licheniformis* from marine sediment, [92] and halocin SH10 produced by an extreme *haloarchaeon Natrinema sp.* BTSH10 from salt pans of South India [93] were reported. Some bacteria particularly those in the digestive tract, produce inhibitory compounds that control the colonization of potential pathogens in fish [94,95].Forinstance a heat-labile and proteinaceous substance with a molecular mass of <5kDa was recovered from *Vibrio* sp. obtained from the intestine of a spotnape pony fish [96]. Similarly, bacteria capable of inhibiting growth of pathogenic *Vibrio* sp. were isolated from the digestive tract of halibut (*Hippoglossus hippoglossus*) larvae [97]. In another study, of the 1,055 intestinal bacteria derived from 7 coastal fish in Japan, 28 isolates (2.7% of the total) inhibited the human and eel pathogen *V. vulnificus*[98].Marked inhibition was displayed by 15 isolates, consisting of 11 *Vibrionaceae* representatives, 3 coryneforms, and 1 *Bacillus* strain NM 12; the latter demonstrating the most pronounced antimicrobial activity. A heat labile siderophore of <5kDa molecular weight inhibited the growth of 227 out of 363 (62.5% of the total) intestinal

bacterial isolates from 7 fish[99]. Bacteriocin producer was also reported from the deep sea shark gut, where a *Bacillus amyloliquefaciens* BTSS3 was shown to produce thermostable, pH tolerant bacteriocin [100]. A detailed view is given in Table 2a and 2b. Fifteen isolates with confirmed consistent antimicrobial activity recovered from Irish seaweeds, as well as sand and seawater, were spore-forming *Bacillus* sp. While PCR screening was successful in identifying three of the marine bacteria as lichenicidin producers, the rest of the isolates did not harbor structural genes for any of the known *Bacillus* bacteriocins for which PCR primers could be designed. These negative PCR outcomes strongly suggest that these isolates produce novel bacteriocins [101].

Bacteriocin classification.

The bacteriocin family includes diverse proteins in terms of size, modes of action, microbial targets and immunity mechanisms. In general, bacteriocins are studied based on the Gram designation of their producing species, Gram-negative Vs Gram-positive (Table 3). Additionally, a relatively small number of bacteriocins from *Archaeal species* have also been characterized.

Table 2aSome characterized marine bacteriocins and their sources

Bacteriocin	Producer strain	Molecular weight	Killing breadth	Source of isolation	Reference
BLIS	*Lactobacillus pentosus* 39	-	*Aeromonas hydrophila, Listeria monocytogenes*	Salmonllets	102
Carnocin U149	*Carnobacterium sp.*	4.5-5kDa	*Lactobacillus, Lactococcus, Pediococcus, Carnobacterium*	Fish	73
Divergicin M35	*Carnobacterium divergens* M35	~4.5kDa	*Carnobacterium, Listeria*	Frozen smoked mussel	75
Divercin V41	*Carnobacterium divergens* V41	4.5kDa	*Carnobacterium, Listeria, Enterococcus*	Fish viscera	74
Carnobacteriocin B2	*Carnobacterium pisciocola* A9b	~4.5kDa	*Listeria*	Cold smoked salmon	82
Piscicocin CS526	*Carnobacterium pisciocola* CS526	~4.4kDa	*Tetragenococcus, Leuconostoc, Listeria, Enterococcus, Pediococcus*	Frozen surimi	76,77
Piscicocin V1a	*Carnobacterium pisciocola* V1	4.4kDa	*Lactobacillus, Listeria, Enterococcus, Pediococcus, Carnobacterium*	Fish	78
BLIS	*Enterococcus faecium* CHG 2-1 and Ch 1-2	-	*Enterococcus*	Venus clams	79
BLIS	*Enterococcus faecium* C-K, C-S, M 2-1, and PEF 2-2	-	*Listeria*	Anchovy, shark fillet, Sword fish fillet	79
Enterocin B like BLIS	*Enterococcus faecium* ALP7	<6.5kDa	*Listeria, Staphylococcus, Bacillus, Enterococcus, Lactobacillus, Lactococcus, Leukonostoc*	Non-fermented shellfish	80
BLIS	*Lactobacillus lactis*	94kDa	*Bacillus, Staphylococcus, Enterococcus, E.coli, Pseudomonas, Shigella*	Sediment sample	81

Table 2bSome characterized marine bacteriocins and their sources

Bacteriocin	Producer strain	Molecular Wt	Killing breadth	Source	Reference
Bacteriocin BL8	*Bacillus licheniformis*	<3kDa	*Staphylococcus aureus, Bacillus sp.*	Sediment	92
BLIS	*Vibrio sp*.	<5kDa	*Bacillus sp., Vibrio sp. Pseudomonas sp.*	Spot nape pony fish	96
BLIS	*Vibrio sp*.			Halibut larvae (Hippoglossus hippoglossus)	97
Bacteriocin	*Bacillus sp*. NM12	Siderophore, <5kDa	*Fish pathogens*	Coastal fish	98
Bacteriocin Bacf3	*Bacillus amyloliquefaciens* BTSS3	~ 3kDa	*Bacillus sp., Staphylococcus aureus*	Deep sea shark (Centroscyllium fabricii)	100
BLIS	*Proteus sp.*CT1.1		*Vibrio*	Cobia	103
BLIS	*Proteus sp.* G1		*Vibrio*	Ornate spiny lobster	103
BLIS	*Bacilllus cereus D9*		*Vibrio*	Subnose pompano	103

Bacteriocins of Gram-negative bacteria. Bacteriocins of Gram-negative bacteria are categorized into four main classes: colicins, colicin-like bacteriocins, microcins, and phage-tail like bacteriocins. [119]. Colicins are so well studied that they have been used as a model system to study bacteriocin structure, function and evolution [120-123].In general, colicins are thermo-sensitive, protease sensitive proteins that vary in size from 25 to 90kDa [124].There are two major colicin types based on their mode of killing; nuclease and pore former colicins. Nuclease colicins (Colicins E2, E3, E4, E5, E6, E7, E8, E9) kill by acting as DNases, RNases, or tRNAses and pore former colicins (colicins A, B, E1, Ia, Ib, K) kill sensitive strains by forming pores in the cell membrane. Proteinaceous bacteriocins produced by other Gram-negative species are classified as colicin-like due to the presence of similar structural and functional characteristics. They can be nucleases (pyocins S1, S2) and pore-formers (pyocin S5) like colicins [125, 126]. S-pyocins of *Pseudomonas aeruginosa*, Klebicins of *Klebsiella species*, and alveicins of *Hafnia alvei* are among the most studied colicin-like bacteriocins. Phage-tail like bacteriocins are larger structures that resemble the tails of bacteriophages which are even argued as defective phage particles [127]. R and F pyocins of *P. aeruginosa* are some examples of the most thoroughly studied phage-tail like bacteriocins [125,128,129].Pore-forming colicins range in size from 449 to 629 amino acids. Nuclease bacteriocins have an even broader size range, from 178 to 777 amino acids. In colicins, the central domain comprises about 50% of the protein and is involved in the recognition of specific cell surface receptors. The N-terminal domain (»25% of the protein) is responsible for

Table 3 Classification of Bacteriocins with examples

	Bacteriocins	Type/Class	Size	Example	Reference
Gram negative bacteria	Colicins	Pore Formers	20- 80	Colicins A, B	104
		Nucleases		Colicins E2, E3	
	Colicin-like		20- 80	S-pyocins	105
				Klebicins	
	Phage-tail like		>80	Maltocin P28	106
		Post translationally modified		Microcin C7	105
			<10	Microcin B17	
	Microcins	Unmodified		Colicin V	107
		Class IIc - non-ribosomal siderophore-type post-translation modification		microcin E492	108
	Class I	Type A- Linear peptides, positively charged	<5	Nisin	109
		Type B- Rigid globular peptides, negatively or neutrally charged		Subtilosin A	110
Gram positive bacteria	Class II	IIa - contain YGNGVxCxxxxCxV, Narrow spectrum of activity		Pediocin, enterocin	111
		IIb – require concerted activity of 2 peptides	<10	Lactacin F, Lactococcin G	111
		IIc – circular peptide bacteriocins		Carnocyclin A	112
		IId – linear, non-pediocin like, single peptide		Epidermicin NIO1	113
	Class III	IIIa – bacteriolysin	>10	Enterolysin A	114
		IIIb – non-lytic bacteriocin		Helveticin A & J	115
Archea	Halocins	Microhalocins	<10	Halocin A4, C8, G1	117
		Protein Halocins	>10	Halocin H1, H4	117

translocation of the protein into the target cell. The remainder ofthe protein is a short sequence involved in immunity protein binding. The killing domain and the immunity region are present in this region. Although the pyocins share a similar domain structure, the order of the translocation and receptor recognition domains are exchanged [123].Finally, Gram-negative bacteria produce much smaller (<10kDa) peptide bacteriocins called microcins. They can be divided into three classes: post-translationally modified (microcins B17, C7, J25, and D93) [130] and unmodified microcins (microcins E492, V, L, H47, and 24). Class IIc bacteriocins are non-ribosomal siderophore-type post-translation modification at the serine-rich carboxy-terminal region, such as microcin E492 [131](Table 3).

Bacteriocins of Gram-positive bacteria. Bacteriocins of gram-positive bacteria are more abundant and even more diverse than those in Gram-negative bacteria [132],but differing in two fundamental ways.

1. Bacteriocin production is not necessarily a lethal event as it is for Gram-negative bacteria.
2. This vital difference is due to the transport mechanisms encoded by Gram-positive bacteria to release bacteriocin toxin. Some have evolved a bacteriocin-specific transport system, whereas others employ the *sec*-dependent export pathway.
3. The Gram-positive bacteria have evolved bacteriocin-specific regulation, whereas bacteriocins of Gram-negative bacteria rely solely on host regulatory networks.

Based on size, morphology, physical, and chemical properties, bacteriocins of Gram-positive bacteria are generally divided into four classes [133].

Class I bacteriocins: Are post-translationally modified small peptides (<5kDa) incorporating non-traditional amino acids such as dehydrobutyrine, dehydroalanine, lantionine and methyl-lanthione called lantibiotics [134]. This class is subdivided into Type A and B with the distinction being that members of Type A are linear peptides (nisin) [135] and positively charged, whereas those in Type B are rigid globular peptides (mersacidin), labyrinthopeptins, such as globular peptide labyrinthopeptin A2 [136] and sactibiotics, such as globular peptide subtilosin A [137] either negatively or neutrally charged.

Class II bacteriocins: Are small 30-60 amino acids (<10kDa), heat-stable peptides that are not post-translationally modified and positively charged [138]. Class II is also subdivided into four subgroups]. The class IIa Listeria-active or pediocin-like peptides containing a conserved N-terminal sequence (YGNGVxCxxxxCxV) or "pediocin box" with two cysteine residues forming disulphide bridge, are the most extensively studied group with a narrow spectrum of activity [139].Lactacin F and lactococcin G are part of Class IIb bacteriocins that require the concerted activity of two peptides to be fully active [140].Class IIc bacteriocins are circular peptide bacteriocins, such as carnocyclin A [141].Class IId bacteriocins are linear, non-pediocin-like, single-peptide bacteriocins, including epidermicin NI01 [142].

Class III bacteriocins: Are generally large (>10kDa), heat-sensitive peptides, subdivided into two subtypes. Type IIIa are bacteriolysins, which are bacteriolytic enzymes such as Enterolisin, which kill sensitive strains by lysis of the cell well [143].Helveticin J (37kDa) produced by *Lactobacillus helveticus* belongs to Type IIIb, which are non-lytic bacteriocins [144].

Class IV bacteriocins. Require lipid or carbohydrate moieties for activity. They are also known as complex bacteriocins, with unique structural characteristics. The first and

last amino acids of these bacteriocins are covalently bound, thus having cyclic structures. Examples include leuconocin S 8 and lactocin 27 [145]. Enterocin AS-48 produced by *Enterococcus faecalis* subsp. *Liquefaciens* S-48 was the first characterized bacteriocin of this class [146].

Bacteriocins of *archaea.* The *Archaea* also produce unique bacteriocin-like antimicrobial compounds called archaeocins [147] but are much less scrutinized than the bacteriocins. So far, two major types of archaeocins have been identified: halocins of halobacteria and sulfolobicins of Sulfolobus genus. Halocins can be divided into two classes based on size: the smaller microhalocins (3.6kDa) and larger halocins of 35kDa [67].The first halocin discovered was S8, which is a short hydrophobic peptide of 36 amino acids, processed from larger 34kD pro-protein. Halocin production is a universal feature of halobacteria [66]. Halocin genes are located on megaplasmids (or minichromosomes). Halocins H4 and S8 are located on ~300 kbp and ~200kbp plasmids, respectively [148, 149].Their activity is usually detected at the late exponential to early stationary growth phase.Sulfolobicins are not extensively studied, Prangishvili et al., [150] screened sulfolobicin production from *Sulfolobus islandicus* isolated from volcanic vents throughout Iceland. This study predicted that sulfolobicin is a membrane associated protein. Sulfolobicins are also associated with membranous vesicles ranging in size from 90 to 180nm in diameter. Like many bacteriocins, they are thermostable and sensitive to protease treatment. Their mode of action is still unknown [151].

5. Antimicrobial efficacy and application of bacteriocins for seafood preservation

Bacteriocins display antimicrobial action against various strainsof pathogen and spoilage microorganisms via a mechanismspecific to each type and class ofbacteriocins [152]. In general, the interaction between the target strain'scell membrane and the (typically cationic) bacteriocins play animportant role in its antimicrobial properties. The electrostaticinteraction created between the negatively charged bacteria cellsand positively charged bacteriocin molecules is necessary forinhibitory effect. However, their ability to kill the bacterial cellsrelies on the interaction of the bacteriocin with bacterial cellmembrane receptor molecules, which vary among the differentclasses and subclasses of bacteriocins [153]. Class I bacteriocins (lantibiotics) have two antimicrobialmechanisms, namely (1) disruption of the integrity of the bacterialcell membrane by forming pores that lead to impairment of themembrane potential and loss of the intracellular components[154], besides (2) enzyme inhibition, which involvesbinding to lipid II (the main transporter of peptidoglycan subunitsfrom the cytoplasm to the cell wall), which causes improper cellwall synthesis and thereby cell death [152]. Themechanisms of antimicrobial properties for class II bacteriocins(non-lantibiotics) differ within the subclasses, but, in general, theycause leakage of cytoplasmic molecules by inducing membranepermeability [152, 155]. For class I bacteriocins, the receptor or docking moleculeis lipid II, while class II bacteriocins interact with the mannoseABC transporter, MptD. However, lacticin Q, a leaderlessbacteriocin, does not need a docking molecule [156]. Instead, high-level membrane permeabilization of targetstrains without requiring specific receptors is the mechanismfor class III antimicrobial action [156]. ForGram-negative bacteria, this interaction is rare or limited becauseof their lipopolysaccharide outer membrane. However, the cellintegrity of these bacteria was reportedly compromised whenbacteriocins were combined with surfactants [152].Bacteriocins have been used to control the growth ofpathogenic and

spoilage bacteria in fish. The use of bacteriocinsalong with other preservatives or methods have led to increasedefficacy in prolonging the shelf-life of fish and fish products.Bacteriocins produced by *Bacillus sp*. isolated from curd exhibitedstrong bactericidal potency against *Salmonella* sp. and *Vibrio* sp. ininfected marine fish *Parastromateus niger*and squid *Loligo duvauceli*[157]. Thisbacteriocin significantly reduced the total bacterial count of theinfected tissues stored at both –4 and –20 °C in a time-dependentmanner. [158] verified that the growthof *Vibrio parahaemolyticus* (inoculated at 10^5 CFU/g) and *L.monocytogenes* (inoculated at 10^3CFU/g) was significantly inhibitedin salted fish fillets (4% NaCl) during storage at 4 °C for 21 days,following treatment with nisin (Ni), *Zataria multiflora* Boiss EO,or their combinations. *V. parahaemolyticus* inoculated in the fishwas completely inhibited by 0.75 mg/mL Ni + 0.405% EO,0.045% EO, and 0.75 μg/ml Ni, at days 2, 6, and9,respectively.In comparison, *L. monocytogenes* increased after treatment withEO and Ni alone but was completely inhibited by combinedtreatment of EO (0.405%) + Ni (0.25 or 0.75 mg/mL) at 1 day.At a very low concentration (1183 IU/g), Ni inhibited the growth of Gram-positive *Lactobacillus plantarum* and *Listeria innocua* in fish homogenates stored at 30 °C [159]. Higher concentrations (>4300 IU/g) were needed against Gram-negative *P. aeruginosa* and *Pseudomonas fluorescens*.This difference was attributed to the impermeable outercell membrane of Gram-negative bacteria, which preventsNi frominteracting with the cytoplasmic membrane [160]. Conversely, a synergistic effect wasexerted on *S. putrefaciens* and an additive effect on *L. innocua* bycombined treatment of chitosan (300 ppm) and Ni (3000 IU/g).[161]developed a novel method using cell-absorbed bacteriocin(that is, a suspension of the *Lactobacillus curvatus* CWBI-B28 bacteriocin-producing cells on which maximum bacteriocins hadbeen immobilized by pH adjustment) that completely inactivated*L. monocytogenes* in contaminated cold-smoked salmon within 3days, and no *Listeria* cells were detected up to 22 days. [162]hindered the initial growth of both anaerobicand aerobic microorganisms in cold-smoked salmon stored at4 °C by wrapping the fish slices with a Ni (500 IU/cm2)-coatedlow-density polyethylene film. However, satisfactory inhibition ofspoilage organisms during long-term storage required the combinedapplication of Ni (2000 IU/cm2)-coated treatment ontovacuum-packed smoked salmon.The application of *Lactococcus lactis subsp*. lactis KT2W2L, a nisin Z producer for biopreservation of cooked, peeled and ionized tropical shrimps during storage at 8˚C was studied [163]. [164] studied the efficacy of bacteriocin producing *Lactobacillus sp*. AMET1506, as a biopreservative for shrimp under different storage conditions. Nisin-coated plastic films suppressed the growth of other aerobic and anaerobic spoilage microorganisms in a concentration-dependent manner [165].Although bacteriocins are widely applied for the preservation of fish, there is limited information on the bio-preservation of mollusks and shrimp, which could be attributed to the limited development of bacteriocins against seafood pathogens [166,167]. One area of active research in seafood aquaculture is the utilization of bacteriocins as antimicrobials.

6. Marine bacteria and bacteriocins for aquaculture

The evaluation of probiotic bacteria capable of producingbacteriocins is an area of intensive research in severalsectors particularly infish farming [168-170]. The rationale of usingmarinebased bacteriocins in aquaculture is based on thefact that the producer bacterial strains occupy more orless the same ecological niche with the pathogens of concern [171,172]. The use of terrestrial bacterial strains as probiotics for aquaculture hashad limited success as strain characteristics of bacteriaare dependent upon the environment in which

theythrive [173,174]. Therefore, isolating bacteriocin producing probiotic bacteria from the marine environment in which theygrow optimally is a better approach as these strains areexpected to be more effective for aquaculture applications compared to the non-marine bacteria. Marine animals are common sources for bacteriocin producingbacteria, and isolation of such strains from sources otherthan marine animals like sea soil, sediment, water, andseaweed were also recorded [175], thussuggesting the diversity of bacteriocinogenic strains fromthe marine environment. Among the major bacteriocinproducers,*Vibrio sp.*,*Aeromonas sp.*,*Pseudomonas sp*.,lactic acid bacteria species, and marine cyanobacteriaproduced bacteriocins possess killing actions that rangedfrom narrow to relatively broad [176-180]. Some of thefindings of these recent studies are summarized inTable 4. It is worth noting as well that among marine animalsharboring bacteriocinproducing bacteria,fishes serve asa major source. The divercins and piscicocins producedby*Carnobacterium spp*. isolated fromfish intestine[192], enterocin P produced by*Enterococcus faecium*isolated from turbot [193] and*Lactococcus lactis*produced nisin F [194] and*Vibrio anguillarum*produced *Vibrio* AVP10 [172], both isolated from catfishesare just among the growing list. Bacterial strains belonging to the genera*Streptococcus*, *Lactobacillus*, *Carnobacterium*, and*Leuconostoc* are usually part of the gastrointestinalmicrobiotaofhealthyfish[177,195 , 196]. This richgreatly accounts forthe frequency of bacteriocin producing strains amongfishes which can be favorably developedfor aquacultureapplications, e.g. incorporation of probiotic strains tofeeds for the convenience of introducing into thefishesdigestive tract.Several isolated marine bacterial strains have shownthe potential characteristics that make them good candidates to become antibiotic alternatives for aquaculturefarming [197,198]. These havebeen shown to be inhibitory towards several knownpathogenicmicrobialstrainsofGram-negativeandGram-positive bacteria [177,180]. The study of [179] features the marine bacterium*Vibriosp*. MMB2strainwhich exhibited a profound inhibition against ashrimp pathogen isolated from marine microalgae. The*Bacillus* speciesbacteriocins are known to have activityrestricted only against Gram-positive bacteria; however,in past few years, new screening results showed theirinhibitory spectrumagainstGram-negativebacteriawhich majorly comprise aquaculture pathogens [200]. Such antagonistic activity againstGram negatives is one of the desirable characteristics of this group,in addition to its sporulating capacity, to be highly consideredfor development as aquaculture probiotics[201].The use of purified bacteriocins foraquaculture farming is still a question mark, as the main concern would then be administering these compounds to the farmedanimals. On the other hand, numerous studies havealready suggested considering bacteriocinogenic strainsto beused as aquaculture probiotics [189,190,202-204]. This isindeed a more sensible approach than direct applicationof purified bacteriocins in view of the fact that the probiotic strains are live cultures and thus able to eventuallyestablish themselves in the hosts and/or the aquatic environment. Possible mechanisms of probiotic bacterialaction as reviewed by [205] include (i)competition for energy or nutrients, ii) competition forspace, (iii) enhancement of the host immune response,(iv) improvement of the water quality, and (v) production of antagonistic compounds.Prophylactic application of probiotic bacteria wasfound to be most efficient for preventing diseases.[206] demonstrated a competitive exclusion effectwithfive probiotic strains versus two pathogens onfishintestinal mucus. They found that the presence of one ofthe probiotics on the intestinal mucus

inhibited theattachment of one of the pathogens tested.It was shownin their study results that previous treatment with theprobiotics displaced the pathogens [206].Other alternatives have also been used to reduce pathogen occurrence in aquaculture (waterfiltration, an addition of sodium chloride, ozonization, and use of UVlight). These techniques have shown to be helpful, butnot having much effect comparable to probiotics [169].*Bacillus spp*. have been successfully used asprobiotics in the aquaculture of black tiger shrimp(*Penaeus monodon*) in Thailand, where it exhibited 47%growth rate improvement and survival rate when challenged with*Vibrio harveyi*. [207] reportedsignificantly improved

Table4Bacteriocins/BLISs isolated within the last 10 years

Producing strains	Bacteriocin/BLIS	Inhibited strains(s)	Isolated from	Molecular mass	References
Lactobacillus fermentum	L. fermentum bacteriocin	*Vibrio parahaemolyticus, Listeria monocytogenes, Listeria sp., Staphylococcus aureus*	Fish gut (Mugil cephalus), prawn muscle (Penaeus monodon)	18 kDa	176
Bacillus licheniformis strain BTHT8	BL8	*Bacillus circulans, Staphylococcus aureus, Bacillus coagulans, Bacillus cereus, Clostridium perfringens, Bacillus pumilus*	Sediment and water samples from off the coast of Cochin, India	1–4 kDa	181
Pseudomonas putida strain FStm2	P. putida strain FStm2 bacteriocin	*Bacillus thuringiensis, Staphylococcus aureus, Escherichia coli, Enterobacter aerogenes, Serratia marcescens, Salmonella spp., Klebsiella pneumoniae, Vibrio parahaemolyticus, Vibrio alginolyticus, Vibrio vulnificus, Vibrio harveyi, Pseudomonas* aeruginosa	Shark skin	32 kDa	178
Lactobacillus fermentum strain SBS001	L. fermentum SBS001 bacteriocin	*Klebsiella oxytoca, Pseudomonas aeruginosa, Escherichia coli*	Water from Vellar estuary, Tamilnadu, India	78 kDa	180
Vibrio spp. MMB2	BLIS	*Aeromonas hydrophila*	Marine microalgal sample (Chlorella salina)	16 kDa, 32 kDa	179
Lactobacillus lactis	L. lactis bacteriocin	*Bacillus subtilis, Staphylococcus aureus, Enterococcus faecalis, Pseudomonasaeruginosa*	Sediment samples from Chennai Harbor, India	94 kDa	182
Lactobacillus casei	AP8 H5	*Escherichia coli, Listeria spp., Salmonella spp.,*	Intestines of Sturgeon fish	5 kDa	177

Lactobacillus plantarum		*Staphylococcus aureus, Aeromonas hydrophila, Vibrio anguillarum, Bacillus cereus*			
Bacillus licheniformis	Lichenicidin	*MRSA, Listeria monocytogenes, Enterococcus faecalis, Salmonella typhimurium, Escherichia coli, Cronobacter sakazakii*	Irish seaweeds (Ulva sp., U. lactuca)		183
Enterococcus faecium ALP7	Enterocin B	*Listeria innocua, Listeria monocytogenes, Staphylococcus aureus, Bacillus cereus, otherLAB*	Marine shellfish	<10 kDa	184
Pediococcus pentosaceus ALP57	Pediocin PA-1/AcH				
Enterococcus faecium	Enterocin	*Listeria monocytogenes, Lb. plantarum, Listeriainnocua, Enterococcus faecalis, Salmonellatyphi, Salmonella paratyphi*	Mangrove environment	5 kDa	185
Bacillus pumilus R2	Pumiviticin	*Salmonella typhimurium, Proteus vulgaris,Micrococcus luteus, wide range of LAB*	Sea soil	3.9 kDa	186
Enterococcus faecalis	E. faecalis bacteriocin	*Staphylococcus aureus, Bacillus subtilis*	Marine environment	94 kDa	187
Bacillus sonorensis MT93	Sonorensin	*Listeria monocytogenes, Staphylococcus aureus*	Marine soil, Parangpettai, India	6,274 Da	188
Lactobacillus acidophilus		*Enterococcus faecalis, Salmonella enterica serovartyphi*	Marine sediments, Caspian Sea		189
Lactobacillus plantarum *Lactobacillus acidophilus*	L. acidophilus bacteriocin	*Lactobacillus bulgaricus, Salmonella enterica serovar typhimurium, Staphylococcus aureus, Bacillus subtilis, Salmonella enterica serovarparatyphi 'B', Escherichia coli, Klebsiella sp.,Serratia marcescens, Pseudomonas aeruginosa*	Gut of marine prawn (Penaeus monodon	2.5 kDa	190
Lactococcus lactis PSY2	Bacteriocin PSY2	*Arthrobacter sp., Acinetobacter sp., Bacillus subtilis, Escherichia coli, Listeriamonocytogenes*	Marine perch fish (Perca flavescens)		191

survival after bacterial invasionchallenge with*Vibrio anguillarumin* Japaneseflounderpreviously treated with commercial probiotic AlchemPoseidon (consortium of*Bacillus subtilis, Lactobacillusacidophilus, Clostridium butyricum,* and *Saccharomycescerevisiae*). These bacterial species were shown to produce potent bacteriocins: bacillocin 22 and a BLIS wereidentified in*Bacillus subtilis*cultures, lactacin and acidocin in*Lactobacillus acidophilus,* and butyricin 7423 in*Clostridiumbutyricum*. Four more bacteriocinogenicspecies including*Bacilluspumilus,Micrococcus luteus,Pseudomonasfluorescens, andPseudomonasputida*arealso currently included in bacterial mixtures that aremarketed as probiotics for aquaculture (Prowins BiotechPrivate Ltd., Hyderabad, India). Recentin vivostudy alsoreported that*Phaeobacter gallaeciensis*, a marine bacterium significantly reduced*Vibrio anguillarumin* culturesof microalgae and rotifers, and prevented vibriosis inCod larvae, suggesting its possible application in aquafarming [208].[209] determined that bathing rainbow trout for 6 days in*Pseudomonasfluorescens*AH2,which was isolated from*Lates niloticus*, reduced mortality from 47 to 32% following challenge with*Vibrio anguillarum* [202]. In a largescale investigation, [210] recovered1018 bacterial and yeast isolates from the skin, gillsand intestine of rainbow trout [202]. Of these, 45 isolates were inhibitory to*Vibrio anguillarumin* a disc diffusion assay. The dominantantagonist was*Pseudomonas*, which improved the survival of rainbow trout against vibriosis following theaddition of cultures to water. Yet,*Pseudomonas fluorescens*AH2, which was regarded as an effective probiotic for rainbow trout conferring protection againstvibriosis, did not protect Atlantic salmon against infection with*Aeromonas salmonicida despite in* vitromethods indicating inhibition of the pathogen [202,211].[212] determined that*Carnobacterium inhibens K1*, which was isolated from the gastrointestinaltract of Atlantic salmon, produced inhibitory substancesactive against bacterialfish pathogens in vitro [202]. The results of in vivo experimentsdemonstrated that the bacteria were metabolically activein both intestinal mucus and the feces of salmonids.Moreover, there was no evidence of any detrimentaleffect on the host [202,213].The value of *Carnobacterium* K was verifiedby [213], who demonstrated antagonismagainst a wide range offish pathogens and confirmedefficacy at reducing mortalities in salmonids caused by*Aeromonassalmonicida, Vibrioordalii*and*Yersiniaruckeri*[202].

Inaddition,thehuman probiotic,*Lactobacillus rhamnosus*53101, was administered at a dose of 109and 1012cells/g of feed torainbow trout for 51 days, and reduced mortalities from52.6 to 18.9% (109cells/g of feed) and to 46.3% (1012cells/g of feed) following challenge with*Aeromonas salmonicida*[214].Moreover, [215,216] noted that A. media A199 controlledinfection by*Vibrio tubiashii*in Pacific oyster larvae. Theculture produced bacteriocin-like inhibitory substancesagainst several pathogenic bacteria in culture media.[202] reported that cultures of*Aeromonas hydrophila*and*Vibrio fluvialis*were effective

atcontrolling infections by*Aeromonas salmonicidain* rainbow trout. [217] conducted a trial to see the effect of bacterial strains isolated from the culturewater of*Penaeus monodon*on the growth of the shrimp larvae. Among the seven strains tested, strain PM-4,added together with a diatom, produced higher survivaland moulting rates of the larvae compared to those ofthe larvae receiving only this diatom. In a biocontrolassay, [218] later proved that the strain PM-4repressed the growth of *Vibrio spp*., most probably byproducing antibacterial substances.[219] also selected naturally occurring beneficial bacteria with the aim to promote the growth and survival ofChilean scalloplarvae*Argopecten purpuratus*. Eleven outof 506 bacterial isolates were found to produce substances inhibitory to a*Vibrio anguillarum*related (VAR) larval pathogen. One of these strains (a*Vibrio sp*.) was ableto protect the scallop larvae against the VAR pathogenin a subsequent challenge [202]. Similarly, a*Roseobacter sp*. strain (BS107) secreted anantibacterial substance against a*Vibrio anguillarum*strain. The antibacterial activity was highest after 48 h ofculturing*Vibrio anguillarum*strain in the BS107 supernatant.Invivo, the cell-free supernatant of the BS107strain significantly enhanced the survival of scallop larvae [220].An *Aeromonas* mediastrain A199 protected the Pacific oyster larvae*Crassostrea gigas*when challenged with*Vibrio tubiashii*[202]. Since time should be considered for the establishmentof probiotic bacterial species on or within the host, it canbe inferred that early exposure of the farmed animals(i.e., egg and larval stages) to the probiotics could resultin protective effects leading to eventual exclusion ofpathogens in the adult stages. In the aquaculture systems,severe microbial problems occur at the egg stage. Manipulating the egg epiflora by subjecting the eggs to bacteriocinogenic probiotics would consequently affect thelarval microflora.Although numerous studies have already shownpromising results regarding the aquaculture potential ofbacteriocins and bacteriocinogenic strains from marinesources, subsequent studies are still needed to confirm itsfeasibility in actualfield and large scale applications andto reinforce its effectiveness by fusing it with existingmethods so as to maximize its potential in the production and protection for aquaculture industry.

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