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# Current developments of bacteriocins, screening methods and their application in aquaculture and aquatic products

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ABSTRACT

The bacteriocins of lactic acid bacteria (LAB) is a kind of antibacterial peptide or protein synthesized by LAB in vivo. They have been the focus of much research because LAB and their metabolic products are generally regarded as safe and have potential application in the aquaculture and aquatic products. At present, the discovery of new bacteriocins involves complicated screening, identification, purification, and characterization processes which impact the application of these bacteriocins. This review summarizes the systematic classification of bacteriocins, especially the bacteriocins inhibiting Gram-negative and Gram-positive bacterium, and the species, genus, family and order of LAB. At the same time, the methods of screening of antimicrobial peptide production are expounded and bacteriocin applications of LAB in aquaculture and storage of aquatic products are described. All of these will provide the faster, easier, and more efficient new antimicrobial explorations and basic knowledge for the development and applications of bacteriocins from LAB.

## 1. Introduction

Bacteriocin of Lactic acid bacteria (LAB) which plays an important role in aquatic production, processing and preservation is a kind of peptide or protein with antibacterial activity (Shuang et al., 2014; Yi et al., 2010). Bacteriocin of LAB is a kind of peptide or protein with antibacterial activity. At low concentrations, it can produce an irreversible killing effect on harmful bacteria. At the same time, they can be biodegraded and digested by the human body, which isn't harmful to health. In contrast to plant extracts and the other protein-based antimicrobial preservatives, bacteriocins that tolerate high thermal stress are active over a wide pH range and remain effective at fairly low concentration. Application of the bactericidal peptides does not alter the sensory quality of food products and reduce the intensity of traditional preservation methods, as the peptides present colorless, odorless, and tasteless characteristics.

Bacteriocins have mainly been derived from LAB, mostly of fermented food origins, and from enteric bacteria such as *Enterococcus faecium* (Enterocin) (Satish Kumar et al., 2011). In contrast, only a few studies of aquatic bacteriocin producers have been performed worldwide, and these have especially targeted aquatic animal-associated bacteria, including several aquatic products such as shellfish (Pinto, 2009), shrimp (Feliatra et al., 2018), fermented Fish (Wang et al., 2018).

The screening of LAB that produces antimicrobial peptides has always been a very difficult and tedious work because of the large number of LAB strains and different culture conditions. The screening process is cumbersome and affected by environmental and human factors (Lin et al., 2013), so only a small part of the species of LAB producing antimicrobial peptides was found. In addition, no culture condition or several specific culture models can accurately determine all strains producing antimicrobial peptides. The establishment of the antimicrobial peptide database provides a new screening method, which is helpful for mining-related new strains and new antimicrobial peptides. In this paper, agar diffusion, polymerase chain reaction, antimicrobial peptide-related gene screening, antimicrobial peptide database screening and fluorescein screening were introduced. Especially, a new generation of antimicrobial agents was discovered by bacterial self-screening with peptide library on the surface (T.Tucker et al., 2018).

In recent years, many useful LAB bacteriocins have been identified and studied in aquatic products, such as enterocin faecium R.A5 (Rim et al., 2016), lactocin lactis strain W2 (Feliatra et al., 2018), plantaricin LPL-1 (Wang et al., 2018), weissellicin 110 (Srionnual et al., 2007), nisin

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Z (Sequeiros et al., 2015), leuconostocin (Rim et al., 2016), paraplantaricin L-ZB1 (Zhao et al., 2014), pediocin PA-1 (Patricia et al., 2016). So far, nisin produced by *Lactococcus lactis* and pediocin produced by *Pediococcus acidilactici* are used as food preservatives commercially. Other effective LAB bacteriocins are in the process of obtaining commercial status to be used as food preservatives (Jiang et al., 2017). This also indicates that the development of LAB bacteriocin requires more research data as a support (such as bacteriostatic mechanism, bacteriocin virulence test, etc.), so as to maximize the value of LAB bacteriocin.

Based upon their advantageous characteristics, bacteriocins have been attracting considerable interest as an alternative natural food preservative to extend shelf life and safety of aquaculture and aquatic products (Johnson et al., 2019). Furthermore, research addressing the presence of LAB in fish, seafood and fish products and their applications has been scarce. The main objective of this review is to update the current status of bacteriocins, screening methods and their application in aquaculture and aquatic products.

## 2. Classification of bacteriocins from LAB

Classification of bacteriocins from LAB is complex and controversial (Ahmad et al., 2017; Cleveland et al., 2001; Djamel et al., 2006). According to the biological, physical and genetic characteristics of bacteriocins and their bacteriostatic effects, they can be divided into four categories (Cleveland et al., 2001) (Table 1).

### *2.1. Class I lactobacillus bacteriocins*

Class I bacteriocins of LAB are antibiotics, and their primary structure contains methyllanthionine and the thioether amino acids Lanthionine (Abba, 2007; Bierbaum, 2009). Such bacteriocins are usually highly effective against Gram-positive bacteria. However, a lot of special bacteriocins of LAB that can restrain Gram-negative bacteria were also discovered, such as *Lactocin Lactis* Strain A5 isolated from broadhead catfish and Paraplantaricin L-ZB1 separated from traditional China fermented sausage, etcetera (etc). These special bacteriocins will also be introduced (Fernández et al., 2007) (Table 1). According to the different morphology, it can be divided into two subclasses: Ia and Ib. The bacteriocins of type Ia are slender and have a molecular weight between 2 and 4 kDa (Deegan et al., 2006). Bacteriocins of class Ib are typical spherical bacteriocins with a molecular weight of 2–3 kDa and a negative charge or no net charge (Djamel et al., 2006).

### *2.2. Class II LAB bacteriocins*

Class II LAB bacteriocins are unmodified and heat-stable peptides from non-lantibiotic bacteriocin with small molecular weight, generally less than 10 kDa. They are non-modified bacteriostatic peptides similar to pediocin. It is divided into the following six subclasses.

#### *2.2.1. Class IIa*

Bacteriocins of LAB IIa are generally composed of 35–50 amino acid residues. The isoelectric point of IIa bacteriocins is generally high with hydrophilic N-terminal (Ennahar et al., 2000; Nissen Meyer et al., 2009); IIa LAB has strong inhibitory activity against *Listeria* spp., so IIa LAB has great application value in dairy products (Braïek et al., 2017; Djamel et al., 2006; Sparo et al., 2006).

#### *2.2.2. Class IIb*

Bacteriocins of LAB IIb (dipeptide bacteriocins) are formed by two different amino acid peptide oligomers, which can be further subdivided into two types, E-type and S-type. E-type is a functional enhancement type, each polypeptide has activity, but the existence of another polypeptide will enhance its bacteriostatic activity (Nissen-Meyer et al., 2011); The S-type is functionally synergistic, and the activity of such LAB bacteriocins depends on two peptide chains. In other words, any single peptide chain has no activity when acting alone, but two peptide chains have antibacterial activity when acting together (Gong et al., 2010).

#### *2.2.3. Class IIc*

IIc bacteriocins are thermally stable cyclic antibacterial peptide carried out of the cell by Leader Peptide (Yang et al., 2014), IIc LAB bacteriocins have a more stable structure, higher heat resistance, more stable protein hydrolysis digestion and wider bacteriostatic spectrum. These bacteriocins can be further divided into two classes: *Mercaptan bactericins* (with two cysteine residues) and *Cystine bactericins* (with only one cysteine residue) (Yang et al., 2014).

**Table 1**
Classification of bacteriocins produced by LAB.

| Producer species | Class | Subclass | Features | Representative | Reference |
|---|---|---|---|---|---|
| *Weissella cibaria* | I | Ia | Slender, 2–4 kDa | Enterocin F4-9<br>Weissellicin 110 | (Maky, 2015; Srionnual et al., 2007) |
| *Lactococcus* sp. | | Ib | Spherical, negatively charged, 2–3 kDa | Salivaricin,<br>lactin 481 | (Deegan et al., 2006; Olivia et al., 2001) |
| *Pediococcus pentosaceus*<br>*Carnobacterium piscicola* | II | IIa | Micrococcus,<br><10 kDa | EnterocinMC13<br>BaCalP57<br>Pediocin PA-2 | (Ennahar et al., 2000; Nissen Meyer et al., 2009; Pinto, 2009; Satish Kumar et al., 2011) |
| *Enterococcus faecium* | | IIb | Dipeptide bacteriocin, pore complex, <10 kDa | Lactacin F,<br>BacALP7 | (Gong et al., 2010; Pinto, 2009) |
| *Enterocin faecium*<br>*Enterocin faecium* | | IIc | Ring type | Garvicin ML | Zhao et al. (2014) |
| *Lactobacillus* spp. ASF360 | | IId | No synthetic preamble and signal peptide, <10 kDa | Lacticin Q | Patricia et al. (2016) |
| *Enterococcus faecium* | | IIe | More than three different amino acid peptides are formed by degradation of larger proteins, <10 kDa | Aureocin A70<br>Garvicin KS<br>Enterococci faecium B3-8 | (Freire et al., 2015; Netz et al., 2001) |
| | | IIf | Other | – | – |
| *Streptococcus equi* | III | IIIa | Thermal instability, bacteriolysis | Zoocin A<br>Lysostaphin | Cotter (2014) |
| *Streptococcus phocae* | | IIIb | Thermal instability, non-lysis | Heleveticin J<br>Dysgalacticin | Vaughan et al. (2010) |
| *Leuconstocaceac latics* | IV | – | Hydrophobic macromolecule with a positive charge | Leuconocin S<br>Uberolysin | (Cotter, 2014; Freire et al., 2015) |

#### 2.2.4. Class IId、IIe、IIf

IId bacteriocins are a class of bacteriocins that do not synthesize N-terminal leading sequences (signal peptides), and other class II bacteriocins that have synthetic N-terminal leading sequences (signal peptides) (Ahmad et al., 2017). IIe bacteriocins are polypeptide bacteriocins composed of three or more different amino acid peptides, which are formed by the specific degradation of large proteins, such as *Aureocin* A70 (Netz et al., 2001) and *Garvicin* KS (Freire et al., 2015). IIf bacteriocins have strong thermal stability, which mainly composed of a combination of single-chain non-pediocin or other bacteriocins, without similar sequences (Zhen et al., 2019).

### 2.3. Class III bacteriocins

Class III bacteriocins are bacteriostatic peptides with high molecular weight (>30 kDa) and poor thermal stability. These bacteriocins can be further divided into IIIa and IIIb. IIIa is the lysogenic bacteriocins, Class IIIb is non-lytic bacteriocins (Cotter, 2014; Vaughan et al., 2010). Class IIIa usually cleaves bacterial cell walls by cleavage to achieve bacteriostasis.

### 2.4. Class IV bacteriocins

Class IV bacteriocins are positively charged hydrophobic macromolecules that form large complexes with other macromolecules (Vaughan et al., 2010). Due to the limitations of existing purification methods, bacteriocins can't be completely separated from complex macromolecules, so the bacteriocins are temporarily classified as class IV bacteriocins. In recent years, some bacteriocins that used to belong to class IV have been reclassified through the combination of isolation method and whole-genome sequencing technology.

By exploring the species, genus, family and order from LAB can better understand the similarity of LAB bacteriocins in performance and classify them. The types and classification of LAB which were favorable for systematic learning and exploration the LAB bacteriocin were described (Table 2).

Recently, a few bacteriocins that can inhibit Gram-positive bacteria isolated from aquatic products have been found. It can be seen that the bacteriocins applied to Gram-negative bacteria in aquatic products in recent years have great prospects and potentials in the application of aquatic products in the future (Table 3). From Egyptian salted-fermented fish isolated from Egyptian salted-fermented fish produces a novel bacteriocin, termed enterocin F4-9. Enterocin F4-9 is modified by two molecules of N-acetylglucosamine β-O-linked to Ser37 and Thr46. The O-linked N-acetylglucosamine moieties are essential for the antimicrobial activity of enterocin F4-9. Further analysis of the enterocin F4-9 gene cluster identified *enfC,* which has high sequence similarity to a glycosyltransferase. The antimicrobial activity of enterocin F4-9 covered a limited range of bacteria, including a Gram-negative strain, *Escherichia coli* JM109 (Maky, 2015). Paraplantaricin L-ZB1 was produced by *Lactobacillus paraplantarum* L-ZB1, which was isolated from the traditional China fermented sausage. Results show that paraplantaricin L-ZB1 could inhibit the growth of microflora, especially *Enterobacteriaceae*, *Pseudomonas* and spore-forming bacteria during sample storage could be used as a suitable biological preservative for chilled rainbow trout fillets (Meng, 2014). LAB strain was isolated on De Man Rogosa Sharpe (MRS) medium from gastrointestinal tissues of broadhead catfish (Clarias macrocephalus). Cell-free supernatant fluid from *Lactococcus lactis* A5 showed inhibitory activities against both Gram-positive pathogens (*Bacillus cereus* and *Staphylococcus aureus*) and Gram-negative pathogens (*Salmonella thyphimurium*). This strain can be used as potential probiotics in animal or aquaculture feeding and the bacteriocin it produces will be useful in food preservative (Azhar et al., 2017).

**Table 2**
Producer species, genus, family and order from LAB.

| Family | Genus | Species |
|---|---|---|
| Lactobacillaceae | Lactobacillus | *Lactobacillus casei* |
| | | *Lactobacillus graminis* |
| | | *Lactobacillus amylophilus* |
| | | *Lactobacillus hominis* |
| | | *Lactobacillus* spp.ASF360 |
| | Pediococus | |
| | Leuconostoc | |
| | Weissella | |
| Enteroccaceae | Pilibacter | *Pilibacter termitis* |
| | Enterococcus | *Enterococcus sp.if-pif* |
| | | *Enterococcus ratti* |
| | | *Enterococcus* sp.BG7-MSG3316 |
| | | *Enterococcus* sp.7F3-DIV0205 |
| | | *Enterococcus faecium* |
| | | *Enterococcus haemoperoxidus* |
| | | *Enterococcus saccharolyticus* |
| | | *Enterococcus faecalis* |
| Streptococcaceae | Lactococcus | *Lactococcus* |
| | Streptococcus | *Streptococcus phocae* |
| | | *Streptococcus meriomis* |
| | | *Streptococcus equi* |
| | | *Streptococcus parauberis* |
| | | *Streptococcus pneumoniae* |
| Streptococcaceae | Streptococcus | *Streptococcus intermedius* |
| | | *Streptococcus iniae* |
| Leuconstoc | Leuconstocaceac | *Leuconstocaceac latics* |
| | oenococcus | *oenococcus kitaharae* |
| Aerococcaceae | Globicatella | *Globicatella sp.HMSC072A11* |
| | Facklamia | *Facklamia miroungae* |
| Carnobacteriacee | Alloiococlus | *Alloiococlus otitis* |

## 3. The screening method of bacteriocins from LAB

Due to a large number of soft acid bacteria, culture conditions, environmental factors and so on, the screening of LAB antimicrobial peptides can be thought to be a complex and difficult task. In order to identify all bacterial strains of antimicrobial peptides more accurately, the screening methods of laboratory antimicrobial peptides are still being explored (Table 4). It provides a new direction to find new laboratory strains and new antimicrobial peptides.

### 3.1. Agar diffusion method

At present, LAB producing antimicrobial peptides were screened by traditional methods. Based on the principle of agar diffusion, the derivative methods are seed method, Oxford cup method and paper method (Pringsulaka et al., 2012). It can be screened by adding a certain concentration of $CaCO_3$ and antibiotics (fungi inhibition) (Castro, 2011). The three-layer plate method is a good method in the agar diffusion method. The first layer is general agar medium containing 1.5% agar and the second layer is Mueller-Hinton medium containing 1.5% agar in the Petri dish. Then, put 5 mL 0.5% agar solution according to 1% (v/v) with sensitive bacteria on the surface of the second layer. Next, the Oxford cups were dispersed on the prepared three-layer solid medium so there was no gap between it and the indicating bacteria solid medium, and put the bacteriocin in these cups. The tablets were moved into the refrigerator at 4 °C for 24 h, and the bacteriocin in the Oxford cup was fully dispersed into the culture medium. Finally, the tablets were removed from the incubator at 37 °C. After about 20 h of incubation and observation, the strains with obvious bacteriostatic circle were filtered and defined as potential bacterial strains producing antimicrobial peptides. Potential antimicrobial peptide-producing bacteria were cultured to neutralize acidity in the liquid medium. Finally, the antimicrobial peptide was determined by the agar diffusion method.

**Table 3**
Bacteriocin inhibiting Gram-negative and Gram-positive bacteria.

| Bacteria | Bacteriocins | Source | Size | Reference |
|---|---|---|---|---|
| *Enterococcus faecalis* F4-9 | Enterocin F4-9 | Egyptian salted-fermented fish | 5,516.6Da | Maky (2015) |
| *Lactobacillus paraplantarum* L-ZB1 | Paraplantaricin L-ZB1 | Fermented sausage | – | Meng (2014) |
| *Lactobacillus pentosus* | Pentocin JL-1 | *Chiloscyllium punctatum* | 2987.23Da | Jiang et al. (2017) |
| *Lactococcus Lactis* | Lactococcus lactis strain PSY2 | Marine perch fish | | Sarika et al. (2012) |
| *Lactococcus Lactis* | Lactocin Lactis Strain A5 | Broadhead catfish | 3.4 kDa | Azhar et al. (2017) |

**Table 4**
Screening and purification method of bacteriocin in aquatic products.

| Bacteria | Bacteriocins | Size | Purification process | Reference |
|---|---|---|---|---|
| *Enterococcus faecalis* F4-9 | Enterocin F4-9 | 5,516Da | PCR method | Maky (2015) |
| *Lactobacillus paraplantarum* L-ZB1 | Paraplantaricin L-ZB1 | – | Agar diffusion method | Meng (2014) |
| *Lactococcus Lactis* | *LactocinLactis* Strain A5 | 3.4 kDa | Agar diffusion method | Azhar et al. (2017) |
| *E. faecium* | BacALP7 | < 6.4 kDa | PCR method | Pinto (2009) |
| *P. pentosaceus* ALP57 | BaCalP57 | < 6.5 kDa | PCR method | Pinto (2009) |
| *P. ehimensis* NPUST1 | *Paenibacillus ehimensis* NPUST1 | < 5.0 kDa | Agar diffusion method | Chen et al. (2019) |
| *Lactobacillus* | *Lactobacillus plantarum* FGC-12 | 4.1 kDa | PCR method | Rim et al. (2016) |
| *Enterococcus faecium* R.A5 | Enterocin faecium R.A5 | | PCR method | Rim et al. (2016) |
| *Enterococcus faecium* R.A73 | Enterocin faecium R.A73 | – | PCR method | Chen et al. (2019) |
| *Lactococcus Lactis* | Lactocin Lactis Strain W2 | – | Agar diffusion method | Feliatra et al. (2018) |
| *Lactobacillus plantarum* LPL-1 | Plantaricin LPL-1 | 4347Da | PCR method | Wang et al. (2018) |
| *Enterococcus faecium B3-8* | Enterocin faecium B3-8 | 5.0 kDa | Agar diffusion method | Lin et al. (2013) |
| *Enterococcus thailandicus* B3-22 | Enterocin thailandicus B3-22 | 6319 Da | Agar diffusion method | Lin et al. (2013) |
| *Enterococcus faecium* MC13 | Enterocin MC13 | 2.15 kDa | PCR method | Satish Kumar et al. (2011) |
| *Weissella cibaria* 110 | Weissellicin 110 | 3,.5 kDa. | – | Shuang et al. (2014) |
| *Lactococcus lactis* TW34 | Nisin Z | 4.5 kDa | agar well diffusion assay | Shuang et al. (2014) |
| *Leuconostoc mesenteroides* R.A76 | Leuconostocin mesenteroides R.A76 | – | PCR method | Chen et al. (2019) |
| *Lactobacillus pentosus* | Pentocin JL-1 | 2987 Da | Agar diffusion method | Jiang et al. (2017) |
| *Lactococcus lactis* | *Lactococcus lactis* strain PSY2 | | Agar diffusion method | Sarika et al. (2012) |
| *Lactococcus lactis* | bacteriocin KTH0-1S | 3.346 kDa | Agar diffusion method | Saelao et al. (2017) |
| *Enterococcus faecium* R.A2 | Enterocin faecium R.A2 | – | PCR method | Rim et al. (2016) |
| *Lactococcus Lactis* | Lactocin Lactis Strain H4 | _ | Agar diffusion method | Feliatra et al. (2018) |

### 3.2. PCR method

With the rapid development of deoxyribonucleic acid (DNA) technology, the amplification of specific genes (polymerase chain reaction (PCR)) has been widely used. A specific antimicrobial peptide can be screened based on the gene sequence of the specific antimicrobial peptide. A certain type of antimicrobial peptide can also be screened according to the conserved genes of antimicrobial peptides. Wieckowicz et al. (2011) performed antibacterial peptide structure gene primer PCR on cheese sample microflora, who proved that the designed primers could be used to detect LAB and LAB producing antimicrobial peptides IIa (Yi et al., 2010). Wang et al. identified two new antimicrobial peptides cerecidin A1 and A7 by PCR screening of *B.cereus* As 1.1846 (Jian, 2014). The type of antimicrobial peptides of LAB can be determined more quickly by PCR technology, but the diversity of antimicrobial peptides structure also brings a lot of work to PCR. However, the PCR based on the structural gene of antimicrobial peptides must be based on the known gene sequences of antimicrobial peptides, which is not conducive to the discovery of new antimicrobial peptides in LAB.

### 3.3. Antibacterial peptide related gene screening method

Colorimetry is a method of determining the content of components to be measured by comparing or measuring the color depth of the solution of colored substances. A colorimetric method based on inhibition and non-indicator which can be used to screen LAB producing bacteriocins. However, based on the color reaction for the formation of colored compounds, the basic requirements for color reaction in colorimetric analysis are as follows: the reaction should have higher sensitivity and selectivity, the composition of the colored compounds generated by the reaction is constant and relatively stable, and the difference between it and the chromogenic agent is large. Based on the colorimetric analysis of phospholipid/polydiacetyl vesicles, 54 strains of LAB and 53 strains of halophytes were screened through high-throughput screening of bacteriostatic agents and halophytes (Yadav et al., 2017). Compared with other traditional methods, this method is more sensitive, rapid and is reliable to the antimicrobial peptides (such as bacteriocins and halouracil) screened from the strains isolated from different natural resources. Therefore, the colorimetric method can be used for screening of bacteriocin production laboratory.

### 3.4. Antibacterial peptide database screening

In recent years, with the development of microbial genomics, it has become a reality to find new antimicrobial peptides directly by using the genetic analysis of LAB in samples. The establishment of a large number of peptide databases not only brings new methods for the development of antimicrobial peptides but also puts forward new directions for the next generation of sequencing work (Stephanie Kate, 2014). Due to the small structural gene fragments and the strong operon diversity of antimicrobial peptides, it provides a new possibility for gene screening of antimicrobial peptides. The opening of peptide linear database also provides a new platform for the screening of antimicrobial peptides. NPP (Natural Product Peptidogenomics) database is a genome development method based on mass spectrometry, which links chemical characterization with biosynthetic genes, objectively compares the mass spectra of antimicrobial peptides with the known library, and assumes the structure and related chemical analysis of antimicrobial peptides (Kersten et al., 2011). By using electrospray ionization/liquid chromatography/mass spectrometry (ESI/LC/MS) technology, Zendo et al. analyzed and compared the spectrum data of known antimicrobial peptides, rapidly analyzed the type of antimicrobial peptides from samples of different sources and whether they contained new antimicrobial peptides (Zendo, 2013). More confirmed the database will be faster and easier to compare.

### 3.5. *Discovery of next-generation antimicrobials through bacterial self-screening of surface-displayed peptide libraries*

Surface Localized Antimicrobial displaY (SLAY) are the platforms that directly assess the functionality of peptides by screening any length, composition, and structure of unlimited numbers peptides in a single tube for antimicrobial activity (Fig. 1) (T.Tucker et al., 2018). Using SLAY, 800,000 random peptide sequences for antimicrobial function were screened and thousands of active sequences were identified. SLAY hits present with different potential mechanisms of peptide action and access to areas of antimicrobial physicochemical space beyond what nature has evolved. Peptides are cloned into the surface display system and transformed into a Gram-negative strain of interest. Peptide surface expression is then induced by IPTG (Isopropyl β-D-1-Thiogalactopyranoside). Bacteria expressing bactericidal or bacteriostatic peptides will decrease in abundance during the induction period. One PCR reaction generates Illumina next-generation sequencing samples for sequencing from plasmid libraries pre- and post-induction. In silico translation and comparison identifies each peptide in the library and its abundance pre- and post-induction to identify potential antimicrobial hits (T.Tucker et al., 2018).

## 4. Application of bacteriocin from LAB in aquaculture and processing

LAB bacteriocins have many applications in aquatic products and aquaculture as follows (Jianming, 2012) (Table 5): First is to feed aquatic animals by adding specific LAB bacteriocins. It can not only inhibit the harmful microorganism produced in the feed but also prolong the shelf life and inhibit the pathogenic bacteria in the aquatic animal body to improve its immunity. Second, bacteriocin is added to the farm as a microecological preparation to improve water quality. The abuse of antibiotics in aquaculture has led to the ecological imbalance of water bodies, which has not only caused a variety of new diseases but also made some microorganisms resistant to antibiotics (Chen et al., 2012; Jianming, 2012; Ozek and Bahtïyarca, 2004; Zhang, 2009). LAB bacteriocin, as a non-toxic, green and efficient bacteriostatic substance, can avoid the micro-ecological imbalance of the breeding environment to the greatest extent in aquaculture and improve the feed intake rate of aquatic animals. The third is to add LAB bacteriocins in the storage and transportation of aquatic products to inhibit pathogenic bacteria and prolong the shelf life. Adding LAB bacteriocins or LAB as biological preservatives to aquatic products can effectively improve product safety and prolong shelf life, and at the same time inhibit the production of biogenic amines, ammonia and trimethylamine oxides in aquatic products (Kuley et al., 2013). bacteriocins application distribution in aquaculture and aquatic products is in the storage of aquatic products (Fig. 2).

### 4.1. *Application of bacteriocins from LAB in aquaculture*

It is great to improve the yield and quality of fish and shrimp by adding specific LAB bacteriocins into the feed. Bacterial diseases are the most common problems in aquaculture, and antibiotics were the most common method in aquaculture before. However, with the development of bacteriocins and the enhancement of human's awareness of environmental protection, bacteriocins from LAB have become the mainstream of preventive biological prevention instead of antibiotics. By adding *P. ehimensis* NPUST1 into the feed of Nile tilapia, it was found that the growth performance, immune function and disease resistance of Nile tilapia were improved (Pinto, 2009). LAB plantarum FGC-12 isolated from the intestine of golden carp was applied to *Penaeus vannamei,* damaging the cell wall of Vibrio parahaemolyticus and inhibiting its reproduction (Chen et al., 2019).

### 4.2. *Application of bacteriocins from LAB in improving water quality*

With the emphasis on environmental water quality, biological control agents have been gradually recognized and respected. It can not only avoid the micro-ecological imbalance of the breeding environment and improve the water quality, but also improve the intestinal flora structure of fish, and improve the quality of breeding biological control agents that people need. LAB bacteriocin as a non-toxic, green, efficient bacteriostatic substance has been discovered and explored. It was found that *Ent. thailandicus* B3-22 produced by the intestinal tract of grey mullet could inhibit the growth of *L. garvieae* strain, improve water quality and avoid the infection of aquatic animals by pathogenic bacteria (Lin et al., 2013).

### 4.3. *Application of bacteriocins from LAB in the storage of aquatic products*

In the storage of aquatic products, many studies have shown that LAB bacteriocin can inhibit pathogenic bacteria and improve the sensory

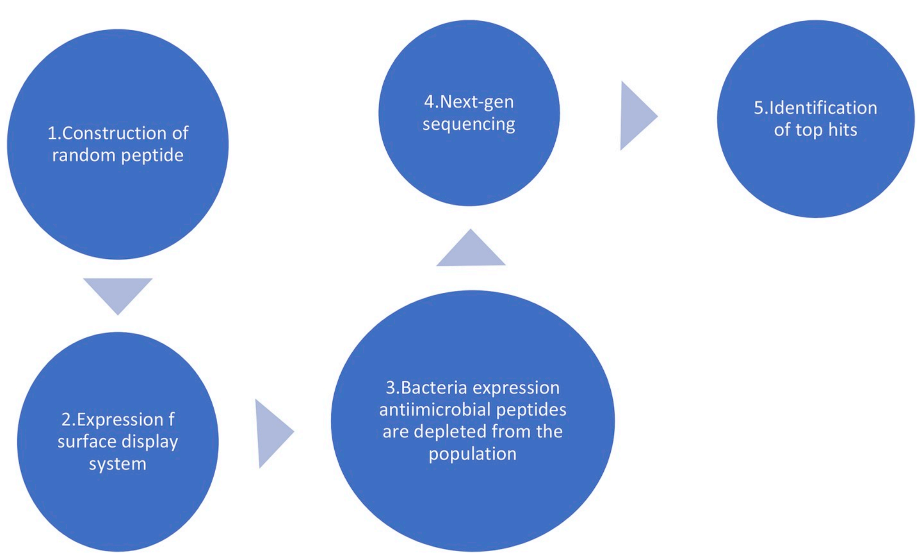


**Fig. 1.** Flowchart for antibacterial peptide database screening.

**Table 5**
Application of bacteriocin in aquatic products.

| Bacteriocins | G−/+ | Application | Source | Inhibited bacteria | Reference |
|---|---|---|---|---|---|
| BacALP7 | + | Reduction of *L. monocytogenes* levels | Shellfish | *L. monocytogenes, Bacillus cereus* etc. | Pinto (2009) |
| BaCalP57 | + | Reduction of *L. monocytogenes* levels | Shellfish | *Staphylococcus aureus* etc. | Pinto (2009) |
| Paenibacillus ehimensis NPUST1 | + | Improve fish immunity | Nile tilapia | Broad-spectrum antimicrobial | Pinto (2009) |
| Lactobacillus plantarum FGC-12 | + | Control of *V. parahaemolyticus* | Golden carp | *V. parahaemolyticus.* | Chen et al. (2019) |
| Enterocin faecium R.A5 | + | Against food-borne pathogens | Tunisian fish | Pathogens | Rim et al. (2016) |
| Enterocin faecium R.A73 | + | Against food-borne pathogens | Tunisian fish | Pathogens | Rim et al. (2016) |
| Lactocin Lactis Strain W2 | + | Biopreservation agents | Shrimp | *Alginolyticus* etc. | Feliatra et al. (2018) |
| Plantaricin LPL-1 | + | Biopreservation agents | Fermented Fish | Foodborne pathogens | Wang et al. (2018) |
| Enteroccin faecium B3-8 | + | Inhibit the growth of *L. garvieae* | Grey mullet | *L. garvieae* | Lin et al. (2013) |
| Ent. thailandicus B3-22 | + | Inhibit the growth of *L. garvieae* | Grey mullet | *L. garvieae* | Lin et al. (2013) |
| Enterocin MC13 | + | Against *Listeria monocytogenes.* | Gut of *Mugil cephalus* | *Listeria* Vibrio vulnificus ect. | Satish Kumar et al. (2011) |
| Weissellicin 110 | + | _ | Fermented Fish | _ | Srionnual et al. (2007) |
| Nisin Z | + | Prevention of *lactococcosis* | Marine fish | Lactococcus lactis | Sequeiros et al. (2015) |
| Leuconostocin mesenteroides R. A76 | + | Against food-borne pathogens | Tunisian fish | Food-poisoning bacteria | Rim et al. (2016) |
| Enterocin faecium R.A2 | + | Against food-borne pathogens | Tunisian fish | Pathogens | Rim et al. (2016) |
| Lactocin Lactis Strain H4 | + | Biopreservation agents | Tiger prawn | Alginolyticus etc. | Feliatra et al. (2018) |
| Bacteriocin KTH0-1S | + | Inhibition of *Staphylococcus aureu* | Fermented shrimp | Staphylococcus aureu | Saelao et al. (2017) |
| Pentocin JL-1 | +/− | Control *Staphylococcus aureus* | Chiloscyllim punctatum | *Staphylococcus aureus* | Jiang et al. (2017) |
| *Lactococcus lactis* strain PSY2 | +/− | Food preservative. | Perch | Gram-positive and Gram-negative bacteria | Sarika et al. (2012) |
| Enterocin F4-9 | − | Fermented fish | Food preservative. | Enterocin F4-8 | Maky (2015) |
| Paraplantaricin L-ZB1 | − | Fermented sausage | food preservative | Enterobacteriaceae, Pseudomonas ect. | Meng (2014) |
| *LactocinLactis* Strain A5 | − | Broadhead catfish | food preservative. | Broad-spectrum antimicrobial activity | Azhar et al. (2017) |

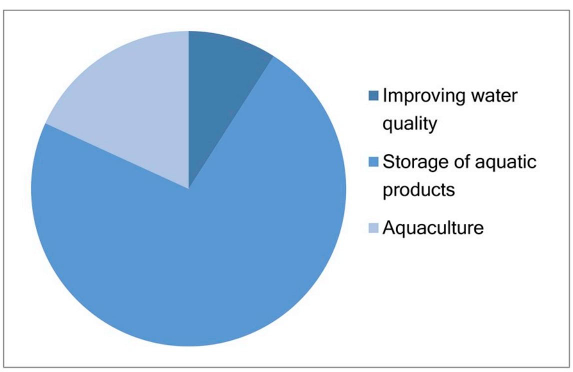


**Fig. 2.** Bacteriocins application distribution in aquaculture and aquatic products.

quality and shelf life of aquatic products (Alzamora et al., 2012; Calo--Mata et al., 2008; Cortesi et al., 2009; Ghanbari, 2013; Pilet and F., 2011; Wang and Zhang, 2015). BaAlP7 and BaCalP57 isolated from shellfish, they inhibited the growth of *Listeria monocytogenes, Listeria monocytogenes, Staphylococcus aureus*, *Bacillus cereus* and other laboratory strains in non-fermented seafood, which could be used as a biological retention strategy to reduce the level of monocyte proliferator in seafood products (Maky, 2015). A bacteriocin producer strain MC13 was isolated from the gut of *Mugil cephalus* (grey mullet) and identified as *Enterococcus faecium* (Pinto, 2009). It inhibits many pathogens that spread in seafood, such as *Listeria monocytogenes, Vibrio parahaemolyticus and Vibrio vulnificus. Enterococcus faecium.* MC13 can be used as a potential probiotic for fish to fight pathogens such as *Vibrio parahaemolyticus*, *Vibrio harveyi* and *Aeromonas hydrophila* in fisheries. It is a valuable seafood biological preservative against *Listeria monocytogenes. Enterococcus faecalis* F4-9 isolated from Egyptian salted-fermented fish produces a novel bacteriocin, termed Enteromycin F4-9. The antimicrobial activity of Enteromycin F4-9 covered a limited range of bacteria including, interestingly, a Gram-negative strain, *Escherichia coli* JM109. Enteromycin F4-9 is sensitive to protease, active at a wide pH range, and moderately resistant to heat (Srionnual et al., 2007). *Staphylococcus aureus* and its drug-resistant strains, which threaten public health and food safety, are in need of effective control by biopreservatives. This Pentocin JL-1 has a broad inhibitory spectrum against both Gram-positive and Gram-negative strains and in particular is effective against multidrug-resistant *S. aureus*. These suggest that Pentocin JL-1 has potential as a biopreservative in the food industry (Jiang et al., 2017). *Lactococcus lactis* KTH0-1S isolated from Thai traditional fermented shrimp is able to produce heat-stable bacteriocin and inhibits food spoilage bacteria and food-borne pathogens (Saelao et al., 2017).

## 5. Conclusions

At present, many new methods of bacteriocin screening have been studied in continuous research and exploration. These methods are often more convenient, which provide a new choice for the complex screening of bacteriocins. Many bacteriocins isolated from aquatic products, such as weissellicin 110, nisin *Z*, plantaricin LPL-1, enterocin MC14, etc. have been found to inhibit Gram-positive bacteria. But many people have also found many special bacteriocins that can inhibit Gram-negative bacteria. For example, enterocin F4-9, paraplantaricin L-ZB1, lactobacillus pentosus, *Lactobacillus lactis* A5, etc. Expanding the scope of inhibitable bacteria has become the focus of current research. This review also introduces the application of these LAB bacteriocins in aquaculture, water quality protection and aquatic products preservation. All these fully illustrate the potential of aquatic products. Many research groups are committed to continuing to explore these issues. In the next few decades, it can be predicted that with its expansion in the global market, the role of many LAB bacteriocins will be found, especially in aquaculture, preservation and water quality protection.

## Declaration of competing interest

The authors report no conflicting interest in any capacity, competing or financial.

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