

# Lactic acid bacteria as probiotics in sustainable development of aquaculture

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**Abstract** – Industrial aquaculture is a dynamic area capable of solving problems of healthy nutrition and food security. Increase of organic pollution, number of opportunistic microorganisms in the aquatic environment of fish farms and the global contamination of feed by mycotoxigenic fungi are serious problems of industrial fish cultivation. The results are weakening of the general condition of fish, immunosuppression, the occurrence of various diseases complicated by drug resistance, the accumulation of antibiotics and chemical compounds in tissues. Probiotics can be an alternative to antibiotics. The use of probiotics is also one of the biological methods for maintaining and restoring the normal physiological state of fish and increasing their productivity. The aim of this review is the scientific justification of the use of lactic acid bacteria as the safest microorganisms in the development of probiotics for aquaculture. The review presented provides criteria for selecting candidate strains for effective probiotics development. The advantages of lactic acid bacteria for the prevention or control of infectious diseases in cultured fish are considered. Lactic acid bacteria are representatives of the fish microbiota, they have antagonistic activity against opportunistic pathogens, fungi and viruses that cause microbiological spoilage of feed, pollute water bodies, and cause diseases of aquatic animals. The review provides information on various researches in which lactic acid bacteria or products derived from them have been used to assess their potential in aquaculture. Numerous scientific studies prove the value of this vast group of microorganisms for the prevention and treatment of fish diseases, for increasing the resistance of aquatic animals to infectious diseases and various stresses, for improving their survival and productivity, and for improving water sanitation in fish reservoirs. Increased use of effective probiotic lactic acid bacteria in aquaculture can make the fish sector safer, more productive and friendly to the environment and human well-being, and will contribute to the sustainable development of aquaculture.

**Keywords:** Probiotic / lactic acid bacteria / fish / aquaculture / production safety / sustainable development

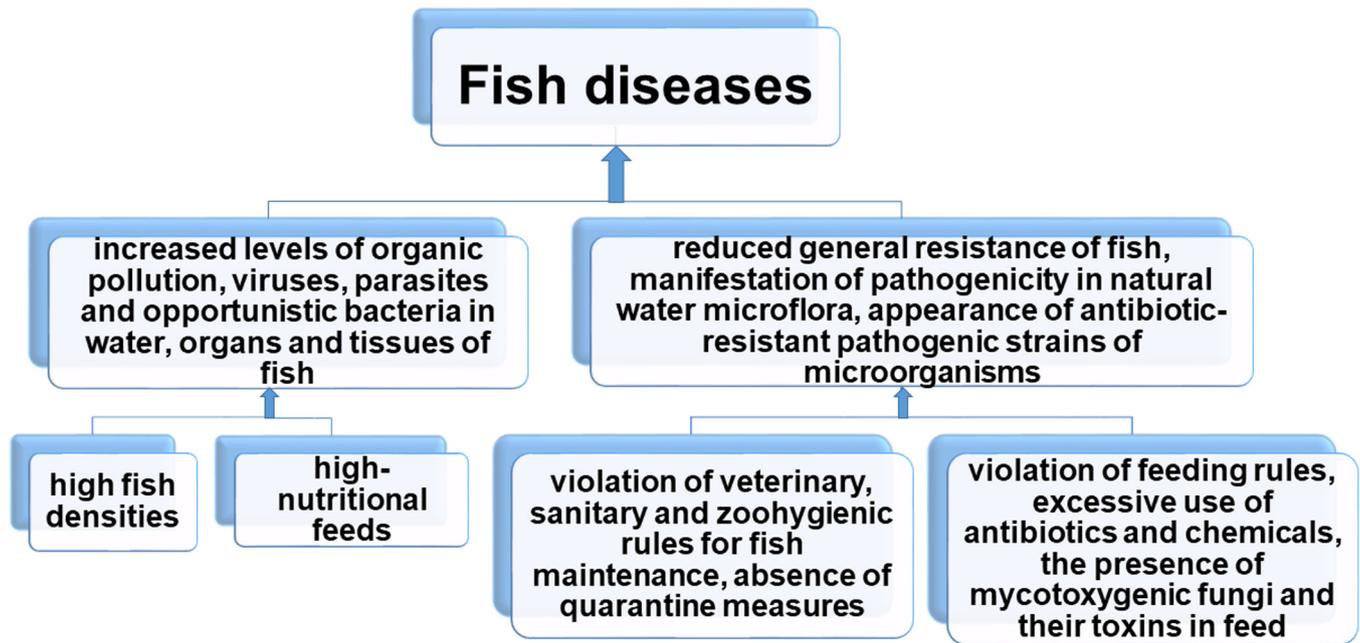
## 1 Introduction

It is expected that in the next few years, as a result of population growth, the development of low-middle-income countries and changing food preferences, the consumption of fish and seafood will increase by almost one third (Thilsted et al., 2016; FAO, 2020). In meeting the demand for safe fish products, global aquaculture will play an increasingly important role among global fish production. Aquaculture is the breeding and cultivation of aquatic organisms (fish, crustaceans, shellfish, and algae) in natural and artificial reservoirs, as well as on specially created marine plantations.

In total, about 600 species of aquatic animals are grown in the world by aquaculture, among which the production of species such as shrimp, bivalve shellfish, salmon, tilapia, carp and catfish is currently expanding (FAO, 2020). Aquaculture is one of the fastest growing food sectors in the world; its production has been steadily growing by 7.5% each year since 1970. In 2018, this sector of fish-breeding was a significant source of fish eaten – 52% (FAO, 2020). Aquaculture production expected to reach 109 million tons by 2030, with more than 90% of that growth coming from low-middle-income countries (World Bank, 2013). The dominance of aquaculture over fisheries is partly due to better control of production processes, better integration into production and supply chains, etc.

However, the FAO predicts that this sector will face enormous environmental challenges in achieving such growth,

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**Fig. 1.** Main factors contributing to fish disease in aquaculture.

requiring a new strategy for sustainable aquaculture development (FAO, 2020). The global trend in aquaculture is the emergence of new pathogens that cause new and unknown diseases, which will spread rapidly, including across national borders, and cause large production losses about every three to five years (FAO, 2019). The rapid expansion of intensive aquaculture worldwide has already led to an increase in the prevalence of transboundary viral, bacterial, parasitic and fungal infections in cultured aquatic organisms, which has affected the sustainability of aquaculture production in many countries (Amal and Saad, 2011; Stentiford et al., 2017). The diseases of aquatic animals in the United States cause economic losses of up to \$6 billion per year and are now one of the main limiting factors for the expansion of the aquaculture industry (Stentiford et al., 2012; World Bank, 2013).

In this regard, there was a need to change the paradigm in working with the biosafety risks of aquaculture. The COFI Aquaculture Subcommittee and the FAO Fisheries Committee at the 10th session in Trondheim (Norway), in August 2019, reviewed and approved a global progressive management program to improve aquaculture biosafety. The new strategy includes innovative technical developments related to feed, genetic selection, bioprotection and disease control, digital innovation, etc. Importantly, the first item of this program is “strengthening the prevention of diseases in aquaculture through responsible fish farming (including reduced antimicrobial resistance in aquaculture and the use of suitable alternatives to antimicrobials) and the use of other scientifically sound technology-proven measures” (FAO, 2020).

In industrial fish farming, aimed at achieving maximum fish growth in a minimum period, there are many reasons for the occurrence of acute diseases that turn into chronic forms, for example overcrowding, high-nutrient feeds, abuse of disinfectants and antibiotics, etc. (Fig. 1). They cause significant economic damage to fish-growing enterprises,

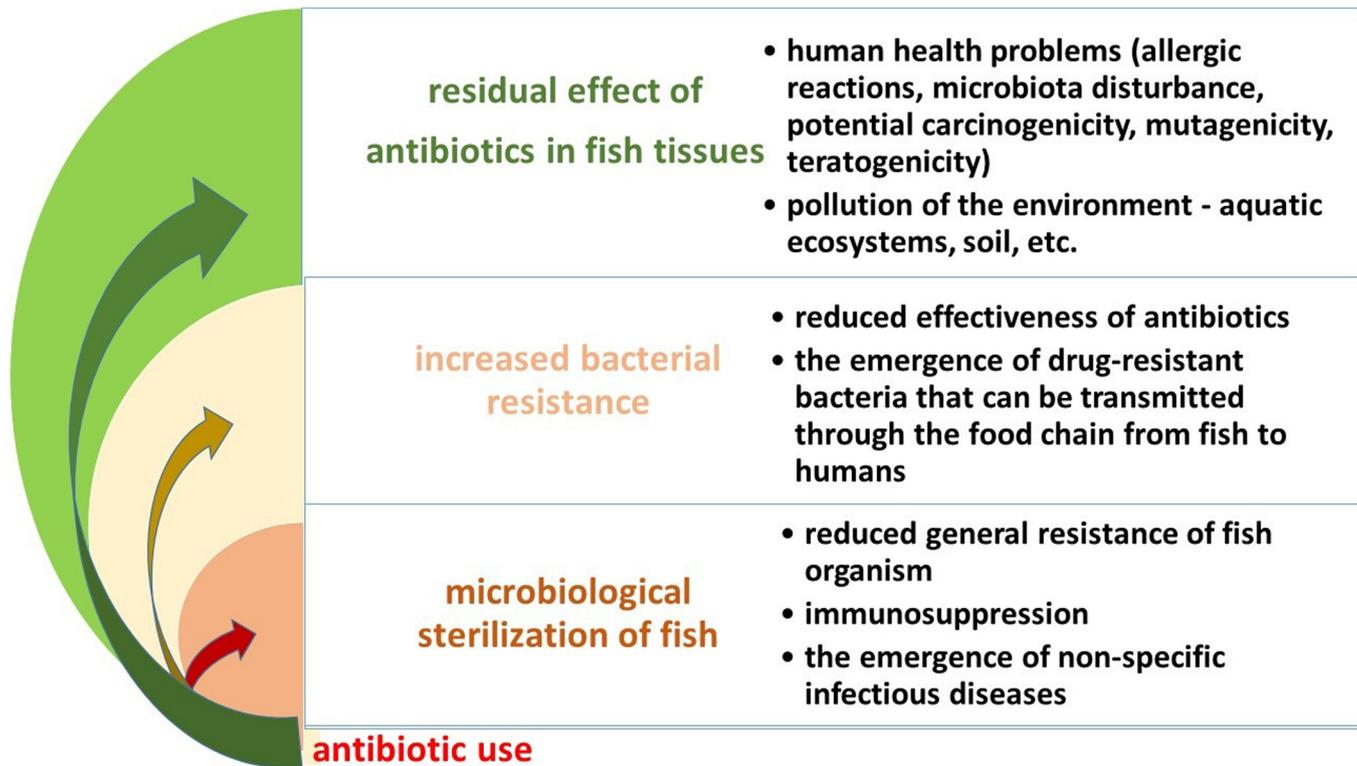
resulting from a decrease in productivity, a slowdown in growth, spoilage of commercial species and fish death.

In industrial fish farming, high planting densities and highly nutritious feeds can lead to an increase in the level of organic pollution and the number of opportunistic bacteria in the aquatic environment of fish farms, as well as in the fish organs and tissues (Borisova et al., 2007). With a decrease in the general resistance of the fish body under the influence of various factors, opportunistic autochthonous microorganisms begin to show pathogenic actions and generate acute diseases that turn into chronic forms, subsequently leading to the fish death (Sergaliev et al., 2019).

Additional causes of fish diseases in aquaculture are violations of veterinary, sanitary and zoohygienic rules for the fish keeping and feeding, together with the lack of quarantine measures for newly imported fish individuals for the purpose of reproduction (Rico et al., 2013).

Excessive unbalance of feed supplements and significant environmental deterioration can disrupt the fish microbiota in aquaculture and cause diseases. When feeding with granulated and extruded, i.e. thermally treated, feeds, aquatic organisms in closed water reservoirs are completely devoid of contact with natural donors of normal microorganisms. Feed, air, and water can be additional sources of toxic substances and pesticides, which disrupt the mucous membrane of various cavities of fish/shellfish and directly affect the microbiota (Ashraf, 2005; Squadrone et al., 2013).

Under aquaculture conditions, many fish diseases also occur due to the presence of mycotoxygenic fungi and their toxins in the feed. Globally, 30–100% of feed samples are contaminated with them (Vila-Donat et al., 2018; Simonova et al., 2020). Various mycotoxins are often found together in contaminated cereals (barley, wheat, corn, and small cereals), corn silage, feed raw materials (meal, cake, etc.), animal and fish feed (Streit et al., 2013; Pinotti et al., 2016; Stanciu, 2017; Li et al., 2018). The



**Fig. 2.** Problems caused by antibiotics in aquaculture.

studies show that co-contaminated samples can have adverse effects on animal health even at concentrations of toxins within limits (defined by FDA (Food and Drug Administration) regulations). This is due to the additive, antagonistic or synergistic effects of the simultaneous presence of several species of mycotoxins in the feed. At the same time, fish are very sensitive to adverse effects of mycotoxins (Anater et al., 2016). For a long time, vaccines and chemicals, including antibiotics, have been commonly used to prevent, treat or control infectious diseases in cultured fish (Cabello, 2006; Rico et al., 2013; Assefa and Abunna, 2018). However, vaccines cannot be used as a universal measure to combat diseases in the field of aquaculture due to the fact that their quantity in a number of countries is limited and their protective effect is manifested only in certain bacterial and viral diseases (Amabile-Cuevas et al., 1995; FAO, 2006). The use of antibiotic agents in aquaculture can cause several serious problems (Tanwar et al., 2014; Cabello et al., 2016; Carlson et al., 2017; Okocha et al., 2018; Gasser et al., 2019), presented in Figure 2 and showing the inconsistency of antibiotics as active agents in the body's fight against emerging progressive diseases.

In this regard, it is necessary to use new preparations to maintain and restore the normal physiological state of fish, which will exert the greatest antimicrobial and fungicidal effect, do not cause resistance of the infectious agent and not have a negative effect on normal fish microbiota.

## 2 Efficacy of probiotics in aquaculture

Probiotics can serve as an alternative antimicrobial agent to reduce dependence on antibiotics, vaccines and other drugs, as

well as to improve the fish health in aquaculture and to obtain safe fish products of high quality, as confirmed by various studies (Wang et al., 2008; Dawood and Koshio, 2016; Banerjee and Ray, 2017; Gobi et al., 2018; Kuebutomye et al., 2019; Soltani et al., 2019; Ringø et al., 2020; Arsène et al., 2021). Probiotics are defined as living non-pathogenic microorganisms that benefit the host when administered in adequate quantities (Steenbergen et al., 2015; Marco et al., 2021). The history of their use in aquaculture began in the mid-1980s (Gatesoupe, 1999), and since then the interest in them in this sector of fish farming has been growing rapidly. The use of probiotics as protective agents prevents the spread of diseases and improves the composition of microbiota (Hoseinifar et al., 2018; Nandi et al., 2018; Doan et al., 2021). Probiotics positively affect the digestion processes, increase feed conversion efficiency and productivity (Merrifield et al., 2010; Doan et al., 2018). Their use makes it possible to improve the condition of the water in the reservoir. In this case, probiotics act in water – direct suppression of the pathogen in culture water (biocontrol) or probiotic biofilter for microbiological maturation of water and displacement of opportunistic bacteria (Al-Dohail et al., 2009; Verschuere et al., 2000). Probiotics enhance innate immunity and resistance to diseases (Grayfer et al., 2018; Feng J et al., 2019; Di et al., 2019; Giri et al., 2021), reduce stress resulting from a sharp change in the composition of the diet, violations of feeding regimes, technological stress and other causes (Taoka et al 2008; Soltani et al., 2017; Dawood et al., 2017).

Fundamental studies of the interaction of probiotics with intestinal microbiota and the body of an aquatic animal have shown that these processes are much more complicated than simply “squeezing out” pathogenic bacteria. Probiotic strains introduced with feed or drugs interact with the host microbiome

(Xia Y et al., 2018), produce metabolites that increase the activity of the host's immune, hormonal and digestive systems (Zhang et al., 2017; Suzer et al., 2008). It has been established that the use of probiotics can have an anti-infectious and immune modulatory effect on the body, increase barrier functions (physiological mechanisms that protect the body from environmental effects, prevent the penetration of bacteria, viruses and harmful substances into it), stimulate motility and excretory functions of the intestine (Son et al., 2009; Talpur et al., 2013; Dawood et al., 2016a, 2017c; Giri et al., 2018). Probiotic together with intestinal microbiota performs the non-specific protection of the intestine against pathogenic bacteria and viruses having genetically determined invasion properties by creating an antagonistic barrier, the so-called colonization resistance of the intestine. By coming into close contact with the intestinal mucosa and covering the surface with a thick layer, it mechanically protects it from the introduction of pathogenic microorganisms.

The antibacterial activity of probiotics is due to the ability to produce alcohols, hydrogen peroxide, lactic, acetic and other organic acids, to synthesize lysozyme and bacteriocins of a wide spectrum of action (lactococin, enterocin, sublancin, aureocin, gassericin, closticin, thuricin, subtilisin, etc.) (Ingolf et al., 2013). They can inhibit the growth of other species also through higher biological potential, rapid reproduction and reaching M concentration, shorter lag-phase, changing pH or redox potential of the medium (Tarakanov, 2000; Bondarenko et al., 2003).

Probiotics, unlike antibiotics, do not adversely affect microbiota and not cause resistance of the opportunistic microorganisms in the gastrointestinal tract of animals, so they are widely used for the prevention and treatment of dysbacteriosis. At the same time, these biologics are characterized by a pronounced clinical effect in the treatment of acute intestinal infections. They reduce intestinal wall permeability disorders caused by bacterial and viral infection, increase the survival of intestinal crypts, reduce apoptosis of the intestinal epithelium, and help maintain the integrity of the cytoskeleton (Sorroza et al., 2013). In addition, probiotics are able to protect against infection due to their lectin-like protein, which exhibits a pronounced inhibitory activity against the production of biofilms by various pathogenic microorganisms (Elayaraja et al., 2014). Biological preparations increase the level of IgA, stimulate the local release of interferon, which facilitates the transport of antigens to the underlying lymphoid cells of the intestinal wall and promotes phagocytosis. Also, they contribute to the suppression of pro-inflammatory cytokines (TNF- $\alpha$ , IL-1 $\beta$ ) and reduce the level of IgE (Elayaraja et al., 2014; Araújo et al., 2016). Probiotic strains are able to inactivate pathogen toxins by enzymatic cleavage and inhibit their binding to receptors, which leads to a decrease in the enterotoxic and cytotoxic effects of pathogens (Baños et al., 2019). The metabolites of probiotic strains do not accumulate in organs and tissues, which makes it possible to obtain environmentally friendly livestock products. Probiotics are safe for the environment and maintenance personnel (Chizhayeva et al., 2017).

Probiotics due to fermentation activity (amylolytic, proteolytic, cellulolytic, etc.), are able to synthesize many biologically active substances: organic acids, alcohols, lipids, vitamins (especially group B), and compounds of the tetrapyrrol structure. Being absorbed into the bloodstream,

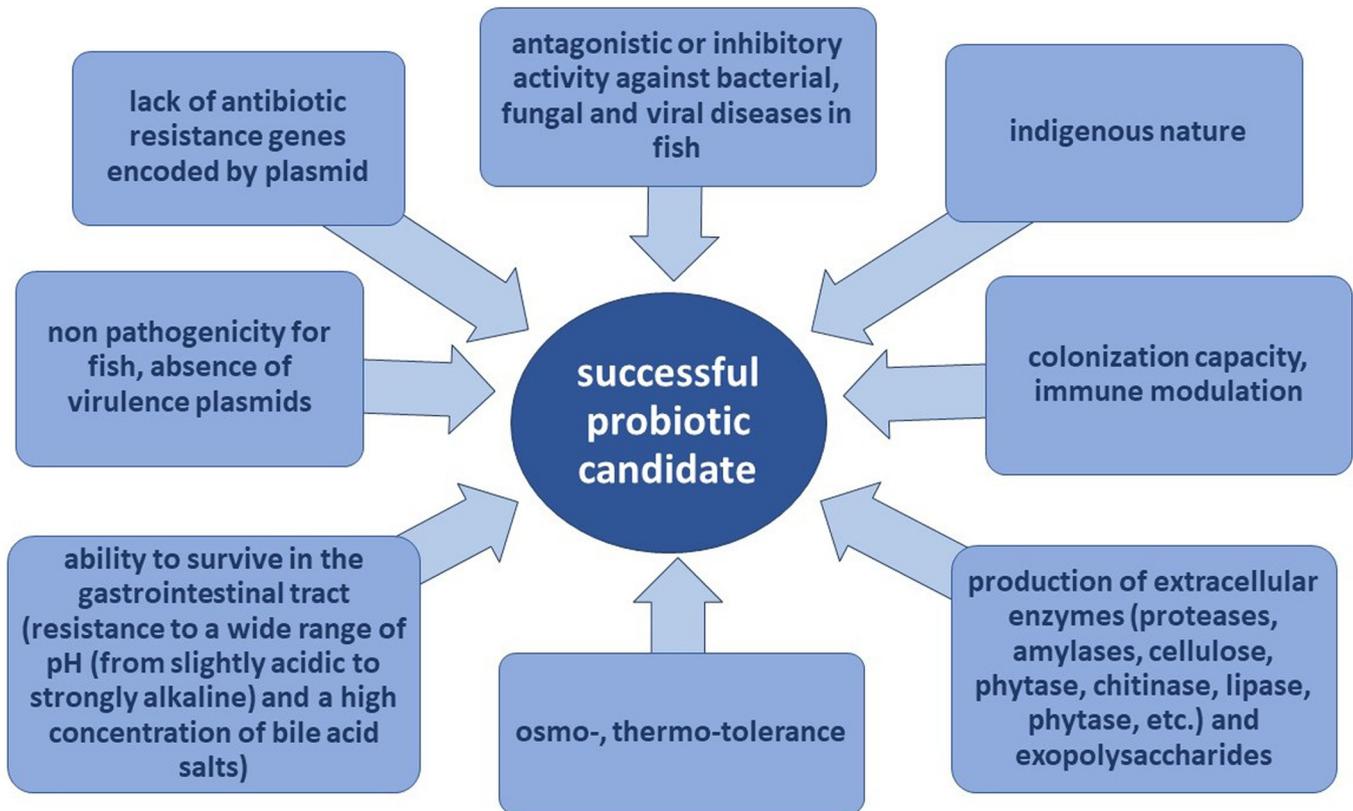
many of them actively participate in energy and vitamin exchanges, playing an important role in the life support of the host organism (Bondarenko et al., 2003). Organic acids enhance the peristalsis and secretion of the intestine, thereby promoting digestion of the feed and increasing the resorption of calcium and iron (Khanongnuch et al., 2018). Polyphosphates of bacteria take part in the transfer of sugars to the cell, performing the function of hexokinases (Nozdrin et al., 2005). At the same time, probiotics are able to synthesize metabolites with antitoxic effects, which reduce the accumulation of heavy metals in water and fish tissues, provide direct protection against oxidative stress caused by metals (Giri et al., 2018). For example, *Lactocaseibacillus rhamnosus* GG and *Limosilactobacillus reuteri* P16 produce exopolysaccharides containing a large number of negatively charged groups (carboxylic, hydroxyl and/or phosphate) that can bind cationic heavy metals such as cadmium and Pb (Halttunen et al., 2007; Giri et al., 2019). In addition, various lactobacilli excrete S-layer proteins, which can also enhance their ability to bind Pb (Monachese et al., 2012). Thus, probiotics bind heavy metals to the surface of their cells and play an important role in the process of natural detoxification and excretion of heavy metals.

Microorganisms commonly used in aquaculture as probiotics include bacteria, yeast and algae (Balcazar et al., 2006). The effectiveness of a probiotic largely depends on the correct selection of candidate strain, which forms its basis (Gueimonde et al., 2013). A successful probiotic candidate for aquaculture must have several important criteria presented in Figure 3 to work well in a variety of aquatic environments – fresh and marine, and in aquatic organisms. Probiotics should be highly tolerant to osmotic pressure, to low and high pH values, and to high bile concentrations; able to inhibit opportunistic microorganisms (Giri et al., 2019).

For the use of probiotic in fish farming, there are no particularly stringent requirements for the source of release of probiotic microorganism. Preferably, the cultures are of an autochthonous nature, but may have a different origin while meeting all the criteria included in Figure 3. Most probiotics are used by feeding, injecting, encapsulating or immersing in water (Chandrakala and Soundharanayaki, 2017; Aydın and Çek-Yılmaz, 2019). Effective probiotics for aquaculture used as a water additive or feed should be representative of microbial communities of fish mucosa, or should have high adhesion or colonization activity.

The skin, gills and intestine are important elements of the fish mucosa and represent a large surface of the first barrier for infections; in addition, their microbiota is responsible for host immunity (Benhamed et al., 2014). Using tilapia as an example, a group of researchers led by Miao Wang (Wang et al., 2020) showed, that using probiotics as additives to water, it is possible to improve the abundance of beneficial host microbiota and the activity of immune enzymes in the immune tissues of the fish mucosa.

The intestinal microbiota should be considered as an independent “organ” that forms during the development of the organism and covers the intestinal wall in the form of a biofilm (Smirnova et al., 2010). The collective immunity of the intestinal biofilm is a strong system that prevents the introduction of foreign strains and does not allow for a full correction of dysbiosis with the help of those preparations of live probiotic cultures that, due to biological incompatibility,



**Fig. 3.** Selection criteria for successful probiotic candidate.

cannot enter the biofilm as a component and replenish the pool of transient bacteria. And yet, in this case, the use of probiotic preparations may be justified. First, when using probiotic microorganisms that are not yet dominant in the normal intestinal microbiota of larvae or growing fish, the effectiveness of their use is explained by the phenomenon of competitive exclusion. Probiotics compete for mucosal attachment sites and for nutrients due to their ability to adhesion or colonization ability (Wang et al., 2008; Hai, 2015). Secondly, various symbionts and parasites are present in the intestinal contents – transient bacteria, protozoa and helminths, whose role in the normal functioning of an aquatic animals organism cannot be underestimated (Merrifield et al., 2015). Probiotic strains introduced into the body of a hydrobiont with feed or water, even being transient, secrete biologically active metabolites, signaling substances, antibiotics and bacteriocins, interact with the microbiota, protozoa and parasites and have a positive effect on the functioning of various physiological systems of the host organism. For transient probiotic bacteria, the most important properties are stability, high enzymatic activity, and the ability to multiply quickly (Chizhayeva et al., 2017).

In addition, probiotics used as a water supplement can improve water quality by affecting the microbial communities of the environment, inhibiting the growth of opportunistic microorganisms, and reducing metabolic waste in the water system (Talpur et al., 2013; Giri et al., 2018). Zhai and other scientists found that lactic acid bacteria and bifidobacteria can bind and remove heavy metals in vitro and in vitro from water and the environment (Zhai et al., 2017; Bhakta et al., 2012).

When ingested with water or feed, probiotics effectively reduce mortality and the accumulation of heavy metals in tissues; improve fish growth rates. They attenuate oxidative stress caused by heavy metal exposure, reverse changes in hematobiochemical parameters, improve innate immunity and restore enzymatic activity of the fish intestinal microbiota (Giri et al., 2018). However, in such cases, it is necessary to regularly administer the probiotic to improve the composition of the microbial community in the culture water and subsequent colonization of the fish mucosa and intestines (Wang et al., 2008).

When using probiotic as a tool to counteract fish diseases in the aquaculture sector, preliminary research work on the frequency and duration of probiotics administration (e.g. daily, daily interval, weekly or weekly interval) is critical to optimize the level of immune responses and disease resistance of aquatic animals against targeted pathogens. An equally important criterion for the effective use of probiotics as an alternative to traditional antibiotics is knowledge of the LD50/LC50 of the target pathogen in the target fish/shellfish, which allows determining the effective dose of the probiotic (Doan et al., 2021). LD50/LC50 is an animal test to determine the level of toxic exposure to substances (in our case, a pathogen). LD50 is an abbreviation used for a dose that kills 50% of the test population (Lethal Dose 50%), and LC50 is an abbreviation used for the concentration of exposure to a toxic substance fatal to half of the tested animals (Lethal Concentration 50%).

Probiotics are often mono-component in composition, i.e. contain one strain of microorganisms. However, studies show that the use of poly-component probiotics (containing several

strains of the same or different species, or genus, or family) may be more effective (Chapman et al., 2011; Xia et al., 2018; Beck et al., 2015). In poly-component or combined probiotics, different microorganisms complement or potentiate each other by enzymatic properties, antagonistic activity, production of biologically active substances, mechanism of action or other properties.

### 3 Advantages of probiotic lactic acid bacteria in aquaculture

A large number of scientific studies presented in Table 1 confirmed that lactic acid bacteria (LAB), which have a number of valuable properties required for probiotic candidates, can be very promising microorganisms for their use in aquaculture. LAB – Gram-positive, homo- and heterofermentative, optionally anaerobic and non-sporeforming microorganisms related to genera *Lactobacillus*, *Pediococcus*, *Enterococcus*, *Streptococcus*, *Lactococcus*, *Vagococcus*, *Leuconostoc*, *Oenococcus*, *Weissella*, *Carnobacterium* and *Tetragenococcus* (Rine et al., 2019; Zheng et al., 2020). LAB are representatives of both human (Yudin et al., 2018) and fish/mollusk microbiota (Ringø et al., 2018; Sergaliev et al., 2019) and have antagonistic activity against opportunistic bacteria, viruses and fungi causing fish and shellfish diseases (Doan et al., 2021; Ringø, 2020).

LAB is safe microorganisms for both animals and humans. They have a GRAS status (generally recognized as safe) declared by the FDA (USA) as well as the status – QPS (qualified presumption of safety) assigned to them by EFSA (European Food Safety Authority) (EFSA Panel on Biological Hazards et al., 2021). However, some researchers note that some bacteria of this large group (*Lactococcus lactis*, *Lc. garvieae*, *Enterococcus sp.*, *Lacticaseibacillus casei* and *Lacticaseibacillus rhamnosus*) may be the causes of bacterial infections (Vesterlund et al., 2007; Protonotariou et al., 2010; Brazca and Bicalho, 2016). Therefore, it is necessary not to neglect the careful assessment of their safety (pathogenicity, virulence, invasive properties, etc.) before introducing strains of LAB into feed probiotics, water supplements or probiotics for fish disease control in aquaculture, because the last instance of this food chain is a human (Nikoskelainen et al., 2003; Ghosh et al., 2017; Le and Yang, 2018; Ringø et al., 2020).

LAB may serve as biological food preservatives due to the antimicrobial activity of their metabolites, such as organic acids (mainly lactic acid and acetic acid), biocides – carbon dioxide (CO<sub>2</sub>), hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), lysozyme, phenyl-lactic acid, fatty acids, antibiotics (reuterocyclin) or bacteriocins (Stoyanova et al., 2012; Kaktcham et al., 2018; Gong et al., 2019; Garcés et al., 2020).

The main product of LAB is lactic acid. Hetero-fermentative lactic acid bacteria produce equimolar amounts of lactic acid, acetic acid/ethanol and carbon dioxide (CO<sub>2</sub>) during fermentation. The antimicrobial activity of lactic acid at low concentrations is not high, especially at neutral pH. Acetic acid is a stronger inhibitor than lactic acid for bacteria, mold and yeast (Reis et al., 2012). Un-dissociated forms of acids diffuse through the wall of the microbial cell due to their hydrophobic nature and then dissociate inside the pathogen cell. From the mixture of acids produced by LAB, lactic acid mainly reduces intracellular pH and inhibits various metabolic functions, while acetic acid

also interferes with cell membrane potential maintenance, inhibits active transport, and damages the cell membrane of pathogens (Ross et al., 2002; Aitzhanova et al., 2021).

Some of the LAB (*Lactobacillus johnsonii* NCC 533, *Lacticaseibacillus paracasei subsp. paracasei*, *Lactobacillus delbrueckii subsp. bulgaricus* etc.) produce hydrogen peroxide H<sub>2</sub>O<sub>2</sub> in the presence of oxygen under the action of flavoprotein-containing oxidases, superoxide dismutase and NADH-oxidase (Marty-Teyssset et al., 2000; Pridmore et al., 2008). The bactericidal effect of H<sub>2</sub>O<sub>2</sub> is explained by its strong oxidative effect on the bacterial cell. Some H<sub>2</sub>O<sub>2</sub>-forming reactions absorb oxygen, thereby creating an anaerobic environment that is not suitable for certain organisms. It is known that CO<sub>2</sub> enrichment in relatively low concentrations enhances the toxic effect of H<sub>2</sub>O<sub>2</sub> on opportunistic microorganisms (Martirosyan et al., 2012).

LAB are known to produce substances with antimicrobial activity such as reuterine, bacteriocins, antifungal peptides, etc. (Kaktcham et al., 2018). Among them, bacteriocins, ribosomally synthesized extracellular peptides or protein molecules with bacteriocidal or bacteriostatic mechanism of action in relation to different types of microorganisms occupy a special place (Pokhilenko and Perelygin, 2011). Initially, bacteriocins produced by different strains were thought to have activity only against other closely related LAB species, but further studies showed their antibacterial activity against more phylogenetically distant Gram-positive and sometimes against Gram-negative bacteria (Pokhilenko and Perelygin, 2011). The spectrum of inhibition by antimicrobial compounds of LAB includes microorganisms that cause fish and shellfish diseases: *Aeromonas salmonicida*, *A. hydrophila*, *Edwardsiella tarda*, *Pasteurella piscicida*, *Vibrio anguillarum*, *V. salmonicida*, *V. harveyi*, *V. parahaemolyticus* and *Yersinia ruckeri*, *Lactococcus garvieae*, *Streptococcus iniae*, pathogenic *E. coli*, fungi *Candida* and mold fungi (Balcazar et al., 2007a; Chomwong et al., 2018; Gong et al., 2019; Ringø et al., 2020).

Many different types of bacteriocins or bacteriocin-like substances of LAB have now been studied and characterized. The most famous are nisin, lactacin B, lactocin 27, plantaricin A, plantacin B and helveticin, leucocin, sacacin, pediocin PA1/AcH, enterocins AS-48, A, etc. (Pokhilenko and Perelygin, 2011; Backialakshmi et al., 2015; Nouri et al., 2015; Eid et al., 2016; Kaktcham et al., 2018). They can affect bacteria by inhibiting cell wall synthesis, increasing cell permeability of target cell membranes, or inhibiting RNase or DNase activities (Galvez et al., 2007). Enterocin AS-48 in combination with NaCl and low temperature is effective against *Staphylococcus aureus* (Ananou et al., 2004). Synergistic action of lactic acid bacteria in combination with organic acid is effective against *E. coli* O157:H7 and *Salmonella typhimurium* (Seo et al., 2013). Bacteriocins (nisin, pediocin and enterocin) in combination with other factors (low and high temperature, hydrostatic pressure, pulse electric fields and salts) inhibited pathogenic bacteria *Staphylococcus aureus*, *Listeria monocytogenes*, *Staphylococcus carnosus*, *Bacillus subtilis*, *Listeria innocua* and *Arcobacter butzleri* (Ananou et al., 2007). Furthermore, Settanni and Corsetti showed the possibility of using bacteriocin-like compounds produced by *Enterococcus faecium* and *Lactococcus lactis* for the storage of plant food due to their low minimum inhibitory concentration against *Listeria spp.* and *Staphylococcus aureus* (Settanni and Corsetti, 2008).

**Table 1.** Beneficial effect of lactic acid bacteria probiotics on aquatic host in aquaculture.

Probiotic species	Aquatic host species	Effect	Sources
Bacterial diseases, immunity, growth, etc. <i>Lactobacillus sp.</i>	<i>Sparus aurata</i> <i>Danio rerio</i>	Produce amylase, trypsin, lipase, alkaline phosphatase and leucine leucinealanine peptidase to improve the feed utilization Provide protection against <i>Aeromonas hydrophila</i> infection	Suzer et al., 2008 He et al., 2017
<i>Lactobacillus delbrueckii</i>	<i>Dicentrarchus labrax</i> L. <i>Cyprinus carpio</i>	Enhancing immunity, growth improvement Enhancing immunity, disease resistance against <i>Aeromonas hydrophila</i> , antioxidant capability and growth performance	Carnevali et al., 2006, Picchietti et al., 2009 Zhang et al., 2017
<i>Lacticaseibacillus rhamnosus</i>	<i>Oncorhynchus mykiss</i> <i>Oreochromis niloticus</i> <i>Oncorhynchus mykiss</i> <i>Portunus pelagicus</i> (Linnaeus, 1758) <i>Pagrus major</i>	Enhance immunity, reduce disease susceptibility and mortality affected by <i>Aeromonas salmonicida</i> Enhance immunity, reduce disease susceptibility and mortality affected by <i>Edwardsiella tarda</i> Improve blood quality Reduce pathogen load in culture tank, improves survival rate and water quality, produce enzymes – protease and amylase Protect from low salinity stress	Nikoskelainen et al., 2003 Pirarat et al., 2006 Panigrahi et al., 2010 Talpur et al., 2013 Dawood et al., 2017c
<i>Lacticaseibacillus rhamnosus</i> and <i>Lactococcus lactis</i>	<i>Pagrus major</i> <i>Oreochromis niloticus</i>	Produce protease to improve feed utilization; promote vitality, weight gain; improve protein and feed assimilation Improving intestinal morphology, enhancing immune status and disease resistance, and affect the gut microbiota of tilapia	Dawood et al., 2016a Xia et al., 2018
<i>Levilactobacillus brevis</i>	Juvenile hybrid tilapia ( <i>Oreochromis niloticus</i> / <i>Oreochromis aureus</i> )	Protect against the toxic effects of <i>Aeromonas hydrophila</i>	Liu et al., 2013
<i>Lactiplantiobacillus plantarum</i>	<i>Oncorhynchus mykiss</i> <i>Paralichthys olivaceus</i> <i>Epinephelus coioides</i> <i>Oncorhynchus mykiss</i> <i>Labeo rohita</i> <i>Seriola dumerili</i> <i>Oreochromis niloticus</i> <i>Cyprinus carpio</i> <i>Oreochromis niloticus</i>	Reduce mortality affected by <i>Lactococcus garvieae</i> Produce protease to improve the feed utilization Improving the growth, immunity, and disease resistance against <i>Aeromonas hydrophila</i> Immunostimulation: significantly up-regulated the expression of cytokine genes, IL-4, IL-12 and IFN- $\gamma$ Improving the growth, immunity, and disease resistance against <i>Aeromonas hydrophila</i> Improve the growth variables and immunophysiological responses, increase resistance to <i>Aeromonas hydrophila</i> Increased survival, remarkably improved the growth performance, specific growth rate, weight gain, final weight, and feed conversion ratio Promoting growth and enhancing innate immune responses and resistance against	Vendrell et al., 2008 Taoka et al., 2008 Son et al., 2009 Perez-Sanchez et al., 2011 Giri et al., 2013 Dawood et al., 2015a Hamdan et al., 2016 Soltani et al., 2017 Doan et al., 2018

**Table 1.** (continued).

Probiotic species	Aquatic host species	Effect	Sources
<i>Lactiplantibacillus plantarum</i> subsp. <i>plantarum</i> and <i>Limosilactobacillus reuteri</i>	<i>Cyprinus carpio</i>	<i>Streptococcus sp.</i> and an iridovirus Enhance stress tolerance Enhance the growth performance, mucosal immune responses, and disease resistance against <i>Aeromonas hydrophila</i>	Giri et al., 2021
<i>Lactiplantibacillus plantarum</i> and <i>Fructilactobacillus fructivorans</i>	<i>Sparus auratus</i>	Increased immunity and protective mechanism under stress conditions, significantly lower cumulative mortality	Liu et al., 2013
<i>Lactiplantibacillus pentosus</i>	<i>Anguilla japonica</i>	Improve immune system and reduce mortality affected by <i>Edwardsiella tarda</i>	Lee et al., 2013
<i>Lactobacillus acidophilus</i>	<i>Clarias gariepinus</i> <i>Carassius auratus</i> <i>Carassius auratus</i> <i>Channa striata</i> <i>Channa striata</i>	Improve water quality, enhance fish health, survival and better feed efficiency and growth performance Biocontrol agent against fish pathogenic bacteria <i>Staphylococcus xylosum</i> , <i>Aeromonas hydrophila</i> and <i>Streptococcus agalactiae</i> Influence on the expression of genes related to immunity, appetite, and on the protein profile of skin mucus. Improve growth and expression of immunoregulatory genes Produces antimicrobial peptide for treatment of <i>Aeromonas hydrophila</i> infections	Al-Dohail et al., 2009 Al-Dohail et al., 2011 Hosseini et al., 2016 Munir et al., 2016 Akter et al., 2020
<i>Ligilactobacillus murinus</i>	–	Produces Bacteriocin, which inhibits of <i>Micrococcus sp.</i> , <i>Staphylococcus aureus</i> , <i>Pseudomonas aeruginosa</i> and <i>Escherichia coli</i>	Elayaraja et al., 2014
<i>Latilactobacillus sakei</i>	<i>Oplegnathus fasciatus</i>	Improve immune system and reduce mortality affected by <i>Edwardsiella tarda</i>	Harikrishnan et al., 2011
<i>Lacticaseibacillus casei</i>	<i>Barbus grypus</i>	Produce lipase, amylase, alkaline phosphatase for enhanced feed conversion	Vand et al., 2014
<i>Lacticaseibacillus paracasei</i>	<i>Takifugu rubripes</i>	Provide protection against <i>Vibrio harveyi</i> infection	Biswas et al., 2013a
<i>Limosilactobacillus reuteri</i>	<i>Cyprinus carpio</i>	Effectively decreased mortality and accumulation of Pb in tissues, improved the growth performance. Alleviated Pb exposure-induced oxidative stress, reversed alterations in hemato-biochemical parameters, improved innate immune parameters, restored intestinal enzymatic activities, and reversed the changes in intestinal microbiota in Pb-exposed fish.	Giri et al., 2018
<i>Lactococcus lactis</i>	<i>Paralichthys olivaceus</i> <i>Cromileptes altivelis</i> <i>Cyprinus carpio</i> <i>Oreochromis niloticus</i>	Activate the innate immune system and protect against pathogen infections affected by <i>Streptococcus iniae</i> , <i>Streptococcus parauberis</i> and <i>Enterococcus viikkiensis</i> . Enhance feed conversion efficiency and weight gain effect Enhancing the growth, immunity, and disease resistance to <i>Vibrio harveyi</i> infection	Kim et al., 2013 Sun et al., 2018 Feng et al., 2019 Xia et al., 2019

**Table 1.** (continued).

Probiotic species	Aquatic host species	Effect	Sources
		Enhancing the growth performance, innate immune response and disease resistance against <i>Aeromonas hydrophila</i>	
		Enhance gut-colonization success, regulate the immune response and larval disease resistance	
<i>Lc. lactis</i> and <i>Leuconostoc mesenteroides</i>	<i>Oncorhynchus mykiss</i> <i>Salmo trutta</i>	Enhancing the immune response and protection against <i>Aeromonas salmonicida</i>	Balcázar et al., 2007 Balcázar et al., 2009
		Improves survival rate, activates phagocytic cells in the head kidney, reduces the rate of proliferation of pathogens in the intestine during <i>Aeromonas salmonicida</i> infection	
<i>Lc. lactis</i> and <i>Lactiplantibacillus plantarum</i>	<i>Paralichthys olivaceus</i>	Significantly improves innate immunity and weight gain, improves survival rate against <i>Streptococcus iniae</i> infection	Beck et al., 2015
<i>Lc. lactis</i> , <i>Lb. plantarum</i> and <i>L. mesenteroides</i>	<i>Oncorhynchus mykiss</i>	Enhancing the immune response and protection against <i>Lactococcus garvieae</i> .	Pérez-Sánchez et al., 2020
<i>Lactococcus garvieae</i>	<i>Oreochromis niloticus</i>	Improves survival rate and inhibits <i>Staphylococcus aureus</i>	Abdelfatah et al., 2018
<i>Enterococcus faecalis</i>	<i>Oncorhynchus mykiss</i> <i>Oncorhynchus mykiss</i>	Enhancing the growth performance, innate immune response and disease resistance against <i>Aeromonas salmonicida</i>	Rodriguez-Estrada et al., 2013 Baños et al., 2019
		Produces enterocin AS-48, which inhibits <i>Lactococcus garvieae</i> and potential alternative for controlling diseases in aquaculture	
<i>Enterococcus faecium</i>	<i>Anguilla Anguilla</i> <i>Anguilla Anguilla</i> <i>Mugil cephalus</i>	Reduce disease susceptibility and mortality affected by <i>Edwardsiella tarda</i>	Chang et al., 2002 Wang et al., 2008 Satish Kumar et al., 2011
		Enhances immunity and improves water quality	
		Produce enterocin MC13, which suppressed <i>Vibrio parahaemolyticus</i> , <i>Vibrio harveyi</i> and <i>Aeromonas hydrophila</i>	
<i>Enterococcus gallinarum</i>	<i>Dicentrarchus labrax</i>	Have moderate protective effect against <i>Vibrio anguil-larum</i>	Sorroza et al., 2013
<i>Enterococcus casseliflavus</i>	<i>Oncorhynchus mykiss</i>	Activate the innate immune system and improve resistance against <i>Streptococcus iniae</i> infection	Safari et al., 2016
<i>Pediococcus acidilactici</i>	<i>Oncorhynchus mykiss</i> <i>Oncorhynchus mykiss</i> <i>Litopenaeus stylirostris</i>	Increase surface area for absorption by increasing villi length	Merrifield et al., 2010b Araújo et al., 2016 Castex et al., 2009
		Produce Pediocin PA-1	
		Increase antioxidant status	
<i>Pediococcus pentosaceus</i>	<i>Epinephelus coioides</i> <i>Litopenaeus vannamei</i> <i>Ctenopharyngodon idella</i>	Enhancing innate immunity, physiological health and resistance to <i>Vibrio anguillarum</i>	Huang et al., 2014 Adel et al., 2017a Gong et al., 2019
		Produce enzymes (amylase, protease and lipase) to improve the feed utilization	
		Promote growth and enhance immune, significantly improves survival rate against <i>Aeromonas hydrophila</i> infection	
<b>Fungal diseases</b> <i>Lactiplantibacillus plantarum</i>	<i>Pangasius hypophthalmus</i>	Inhibition of the growth of the parasitic <i>Saprolegnia parasitica</i>	Nurhajati et al., 2012
<b>Viral diseases</b>			

**Table 1.** (continued).

Probiotic species	Aquatic host species	Effect	Sources
<i>Lactobacillus sp.</i>	<i>Paralychthys olivaceus</i>	Develop resistance against lymphocystis disease virus (LCDV)	<a href="#">Hari Krishnan et al., 2010</a>
<i>Lactiplantibacillus plantarum</i>	<i>Epinephelus coioides</i>	Enhancing innate immune responses and resistance against iridovirus	<a href="#">Son et al., 2009</a>

**Table 2.** Lactic acid bacteria application in aquaculture and its effect on reproduction of aquatic host.

Probiotic species	Fish species	Effect	Sources
<i>Lacticaseibacillus rhamnosus</i>	<i>Danio rerio</i>	Induced remarkable changes in the maternal and zygotic control of F1 fish, enabling them to undergo a faster and more successful embryonic development. Induce follicles maturation process Enhance follicles development and embryo quality Estradiol receptor, vtg, cyclin B, activin $\beta$ A1, smad2 gene expression increase Enhance gonadal growth, fecundity and embryo survival Enhance sperm count	<a href="#">Miccoli et al., 2015</a> <a href="#">Gioacchini et al., 2012</a> <a href="#">Carnevali et al., 2013</a> <a href="#">Gioacchini et al., 2011b</a> <a href="#">Lombardo et al., 2011b</a> <a href="#">Vílchez et al., 2015</a>
	<i>Danio rerio</i>		
	<i>Danio rerio</i>		
	<i>Danio rerio</i>		
	<i>Fundulus heteroclitus</i>		
	<i>Anguilla anguilla</i>		
<i>Pediococcus acidilactici</i>	<i>Carassius auratus</i>	Improvement of reproductive functions – high percentage and duration of sperm motility, absolute fertility and success of fertilization	<a href="#">Mehdinejad et al., 2018</a>
<i>Lacticaseibacillus rhamnosus</i> and <i>Lacticaseibacillus casei</i>	<i>Danio rerio</i>	Up-regulate the expression of leptin, kiss2, gnrh3, fsh, lh, hcgr, and paqr8 genes responsible for fecundity and follicle maturation	<a href="#">Qin et al., 2014</a>

The antibiotic reuterocyclin from *Limosilactobacillus reuteri* in combination with bacteriocins, such as enterocin AS-48, nisin or lacticin 481 has a strong synergistic effect against growth of *Listeria monocytogenes*. There is also a higher antibacterial activity of nisin in combination with reuterin (secondary metabolite) against *S. aureus* ([Arques et al., 2008](#)). Bacteriocins of lactic acid bacteria are non-toxic to animals and humans, do not change nutritional properties of food products, are effective at low concentration and do not lose activity during cooling or heating ([Akbar et al., 2016](#)).

Antifungal peptides of LAB show potential antifungal properties against mycotoxigenic fungi of the genera *Aspergillus*, *Fusarium*, *Penicillium* and *Rhizopus*, as well as inhibition of mycotoxin synthesis and detoxification of mycotoxins in plant raw materials from which fish feed is produced, which is important for the fish sector ([Khalil et al., 2013](#); [Muhialdin et al., 2020b](#)). Gourama and Bullerman ([Gourama and Bullerman, 1995](#); [Gourama, 1997](#)) reported antifungal and antiaflatoxin properties of lactic acid and other

active metabolites of LAB. *Lactiplantibacillus plantarum* releases phenyl lactic and 4-hydroxyphenyl lactic acids that have antifungal activity ([Lavermicocca et al., 2000](#)). Similarly, Dalie and others ([Dalie et al., 2010](#)) observed growth inhibition of *Fusarium proliferatum* and *F. verticillioides* by *Pediococcus pentosaceus* L006 isolated from maize leaf. LAB strains have the ability to detoxify mycotoxins by binding them to polysaccharides and proteins, components of the cell wall ([Wang et al., 2015](#)). Some scientists have proven the ability of *L. acidophilus* VM 20 and *Bifidobacterium animalis* VM 12 to detoxify aflatoxin B1, patulin and ochratoxin A in aqueous solution ([Peltonen et al., 2001](#); [Fuchs et al., 2008](#)). The antifungal activity of *Pediococcus acidilactici* and *Pediococcus pentosaceus*, as well as their ability to inhibit the formation of zeralenone ([Mandala et al., 2007](#); [Muthulakshmi et al., 2016](#)), has been determined. Nurkhayati et al. proved the inhibitory effect of *Lactiplantibacillus plantarum* FNCC 226 against *Saprolegnia parasitica* on catfish *Pangasius hypophthalmus Sauvage* ([Nurkhayati et al., 2012](#)).

LAB in numerous *in vitro* and *in vivo* studies show potential antiviral activity against respiratory and gastrointestinal viruses such as rotaviruses, noroviruses, enteroviruses, and salmonid viruses (Nácher-Vázquez et al., 2015; Nishihira et al., 2018; Seo et al., 2020; Muhialdin et al., 2021). Researches by Harikrishnan et al., have shown that the use of dietary probiotic *Lactobacillus sp.* generated resistance to lymphocytic disease virus (LCDV) in *Paralichthys olivaceus* (Harikrishnan et al., 2010). Son V.M. and his team of researchers confirmed that dietary administration of the probiotic *Lactiplantibacillus plantarum* enhanced the innate immune responses and resistance of the grouper *Epinephelus coioides* against iridovirus (Son et al., 2009). Many researchers attribute the mechanism of antiviral activity of LAB to direct contact with the virus, suppression of viral replication regulation by inducing expression of antiviral genes, or stimulation of host immune system functions (Nakayama et al., 2014; Arena et al., 2018). In Y. Jung team studies it has been shown that administration of high doses of *Lacticaseibacillus casei* promoted rapid induction of antibodies IgG1 and IgG2a, innate immune cells and cytokines (Jung et al., 2017).

Lactobacteria support humoral and cellular immunity, stimulate the release of lysozyme, activate phagocytosis, which increases the overall level of body protection against infections (Sandes et al., 2015; Mojgani et al., 2020). In addition, they have the ability to absorb substances that cause allergic reactions and hypersensitivity to food components. They are involved in the formation of the phenomenon of “oral tolerance” to food antigens, that is, they help the body with food allergies.

The antioxidant activity of LAB also deserves special attention in the aspect of their use in aquaculture. Castex et al., in their studies have shown the effect of dietary probiotic *Pediococcus acidilactici* on increasing antioxidant protection and reduced levels of oxidative stress of shrimp *Litopenaeus stylirostris* (Castex et al., 2009). W. A. Abd El-Ghany in its review showed that intracellular compounds of LAB are able to inhibit lipid peroxidation and show resistance to hydrogen peroxide and hydroxyl radicals, as well as to glutathione peroxidase activity. The mechanism of antioxidant effects in his opinion is associated with an increase in the content of uronic acid, as well as the chelating ability of the iron ion, which is involved in the formation of free radicals, and production of antioxidant enzymes – glutathione peroxidase, superoxide dismutase, and nicotinamide adenine dinucleotide oxidase and peroxidase (Abd El-Ghany, 2020). A. Humam and others reported on the antioxidant activity of *Lactiplantibacillus plantarum* triggered at thermal stress (Humam et al., 2019).

Production and availability of extracellular enzymes such as proteases, carbohydrases, amylases, lipases and phytases in LAB contribute to the fact that probiotics based on them positively affect the growth rate of the host (Gatesoupe, 1999; Grayfer et al., 2018) improving digestibility of the feed (Kim et al., 2007).

Reproductive health and quality of fish gametes is a very important issue for fish farming, especially for highly breeding species, since most of them show poor quality of gametes. The previous studies have shown that some LAB, presented in Table 2, had a positive effect on the reproduction of aquatic animals. These probiotics enhanced gonadal growth (Lombardo et al., 2011b), induced follicles maturation process (Gioacchini et al., 2012), contributed to ovulation and fertility;

increased count and quality of sperm and eggs, and promoted hatching and survival of embryos and larvae (Miccoli et al., 2015; Vilchez et al., 2015; Mehdinejad et al., 2018; Aydin and Çek-Yalmaz, 2019).

Thus, there is a growing body of experimental evidence that the health, zootechnical performance of cultured aquatic animals and cultured water quality can be improved through the prophylactic use of probiotics.

## 4 Conclusion

Aquaculture is one of the most dynamically developing areas of fisheries, designed to meet the needs of a growing population for protein. However, a serious problem hindering the growth of production in this sector of fish farming is infectious diseases of fish and shellfish. To solve it, it is necessary to search for new environmentally friendly antimicrobials that are alternative to antibiotics and chemicals, while at the same time effectively ensuring the prevention and control of diseases of aquatic animals.

Probiotics are one of the antimicrobial alternatives to antibiotics. They are effective in the prevention and treatment of gastrointestinal diseases of bacterial etiology, after antibiotic therapy and vaccination courses, and in reducing economic losses during feed changes or transportation. LAB are popular probiotic strains used to combat bacterial, fungal and partly viral pathogens. Their action is aimed at increasing immunity, digestion, protection against pathogens, and promoting growth and reproduction of fish and shellfish. Numerous studies have shown that probiotics can serve as an alternative to antibiotics. Of course, it is impossible to refuse vaccinations, disinfections, and the use of antibiotics, anthelmintic and coccidiostatics with appropriate indications. Still, it is necessary to restore the normal microbiota after their application. If the mucous membrane of the digestive tract and normal gut microbiota are damaged, the effective production is impossible, since the nutritional feed components simply cannot be absorbed.

Thus, probiotics based on LAB, the beneficial properties and *in vitro* and *in vivo* safety of which have been thoroughly investigated, are very effective, environmentally friendly and suitable for the entire aquaculture system (basic and supplementary nutrition, water purification, prevention and treatment of diseases), and positively affecting the health, productivity, and sustainability of hydrobionts and consumer health.

## Conflict of interest

All authors declare no conflicts of interest in this paper.

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