



Probiotics in aquaculture: a promising emerging alternative approach

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Abstract

Aquaculture is an important food producing sector to fulfill nutritional food demand of a continuously growing population. However, disease outbreak has become a major problem in aquaculture which cause huge economic loss to aquaculture industries. The use of expensive chemotherapeutic drugs for treatment have negative impacts on the aquatic environment. So there is a growing concern to find other safe, non-antibiotic based and eco-friendly alternative for the treatment of the diseases. The use of probiotics is a promising alternative approach for the control of infectious agents and treatment of diseases. The benefits of probiotic include stimulation of growth, improved digestion, enhanced immune response and recuperate the water quality as well. Probiotics concoct the fish to fight against various pathogens and improves the overall health as they show anti-bacterial, anti-fungal and anti-viral properties. The use of probiotics in aquaculture is a recent trend and its efficacy in aquatic environment has not been studied extensively. This review paper provides the current knowledge of the use of probiotics in aquaculture, selection criteria, types of probiotics used in aquaculture, their mode of action and administrative methods of probiotics in aquaculture.

Keywords Putative probiotics · Prebiotics · Synbiotics · Antibiotics · Carp · Quorum sensing

1 Introduction

Aquaculture is an important and rapidly growing sector as it plays an important role to achieve global protein food demand compared to capture fisheries and terrestrial farmed meat. The role of aquaculture to improve the socio-economic status of any region is highly appreciable because it is not only limited to the source of essential nutrients but it also generates various employment opportunities (Araujo et al. 2015; Handbook on Fisheries Statistics 2014). India ranks second in the world after China in fish production through aquaculture with a contribution of 6.3% of the global aqua production, which is very less as compared to that of China (60.5%) (Chavan 2018; Mo et al. 2018). Fishes are dominant in aqua products, and around 200 fish species are produced for their commercial value (Swapna et al. 2010).

With the increasing intensification and commercialization of aquaculture production, diseases have become a hurdle in the fish farming industry (Hai 2015). The most common disease causing bacterial pathogens among aquaculture are gram-negative such as, *Aeromonas*, *Flavobacterium*, *Pseudomonas*,

Vibrio and *Yersinia species*. These pathogens are etiological agents of various diseases like, enteric red mouth disease, furunculosis, hemorrhage, septicemia, vibriosis and so on (Hamid et al. 2017; Cascales et al. 2016; Patra et al. 2016; Wiklund 2016; Ronneseth et al. 2017). The use of chemotherapeutic drugs has served as an option to cure common diseases prevailing in fish farming (Hambali and Akhmad 2000).

In aquaculture, chemotherapeutic agents like antibiotics and chemicals are the classical cure for microbial infection. However, the extensive usage of these chemotherapeutic drugs leads to their accumulation in aquatic habitat and results in harmful consequences such as emergence of antibiotic-resistant bacteria, accumulation of antibiotic residues in the flesh, kill the beneficial microbes of the gastrointestinal tract and alterations in microbiota (effect on non-target microbes) of the aquatic environment (Munoz-Atienzal et al. 2013; Azevedo et al. 2015). Therefore, the use of antibiotics as chemotherapeutic drugs in aquaculture has become risky (Balcazar et al. 2008; Mancuso et al. 2015; Balcazar et al. 2006a, b). The quest for better alternatives to prevent infection and replace the antibiotics has been a major concern now-a-days.

A promising emerging alternative approach to prevent fish diseases is the use of probiotics, which helps fishes to fight against pathogens by various mechanisms. The importance of probiotics used in aquaculture is not only limited to gastrointestinal tract, but it also plays a major role in the improvement

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of overall health of an organism (Mehrabi et al. 2018) such as: it acts as growth promoter (Gobi et al. 2018), prevents the diseases (Meidong et al. 2018), enhances the immune response (Havenaar and Marteau 2018; Ramesh and Souissi 2018) and improves the water quality by modifying microbial community of water and sediments (Verschuere et al. 2000; Deng et al. 2018). In ponds, nitrogenous contaminants like ammonia and nitrate have become a serious concern. Previous reports show that the use of *Lactobacillus* species as probiotics removes the nitrogenous waste from the ponds and use of *Bacillus* species improves the water quality by converting organic carbon to slime (Ma et al. 2009; Verschuere et al. 2000; Kolndadacha et al. 2011). Khattab et al. 2005 have reported the use of *Micrococcus luteus* as probiotics which resulted in increased growth performance and improved feed conversion ratio (FCR) in Tilapia (*Oreochromis niloticus*). Sakata 1990 and Ringo et al. 1995 have demonstrated the role of *Bacteroides* species, *Clostridium* species, *Agrobacterium* species, *Brevibacterium* species and *Microbacterium* species as nutritional sources to the host by supplying fatty acids and vitamins.

This review aims to provide useful knowledge about the use of probiotics in aquaculture, selection criteria, most commonly used probiotic strains, their possible mode of action and administrative methods in aquaculture.

1.1 Definition and brief history of probiotics

In 1907, Elie Metchnikoff, a Russian analyst observed that Bulgarian workers had a long life as they consumed fermented milk products. Later in 1965, Lilly and Stillwell explained the concept of probiotics, as a substance which accelerates the growth of good microbes. Parker (1974) gave the definition of probiotics as “organisms and substances, which add to intestinal balance”. Fuller (1992) refined the definition as, “A live microbial feed supplement that beneficially affects the host by improving its intestinal microbial balance”. This definition signifies that the living bacterial cells are an imperative part of potential probiotics and also clarifies the confusion created by the use of term “substance”. WHO (2001) has termed probiotics as live microbes, which when administered in sufficient amount, confer a health benefit to the host.

Probiotics protect the host organism from pathogenic bacteria by liberating metabolites like bacteriocins and different organic acids. These metabolites hinder the adhesion of different pathogens and also inhibit them by limiting the available resources such as nutrients and space (Servin and Coconnier 2003; Vine et al. 2004). Probiotics have the potential to improve the host's defenses, including the innate and acquired immunity system. This is important for the prevention and treatment of infectious diseases and also to cure inflammation in the digestive tract. Probiotics also have a direct influence on other microbes, either commensal or pathogenic,

which is very important for the prevention, treatment and restoration of the bacterial equilibrium inside the gut of the host (Oelschlaeger 2010). The use of probiotics in humans, pigs, steers and poultry has already been studied, but the use of probiotics in aquaculture is relatively a new concept (Daniel 2017; Chua et al. 2017; Jiang et al. 2017; Harimurti and Hadisaputro 2015; Uyeno et al. 2015).

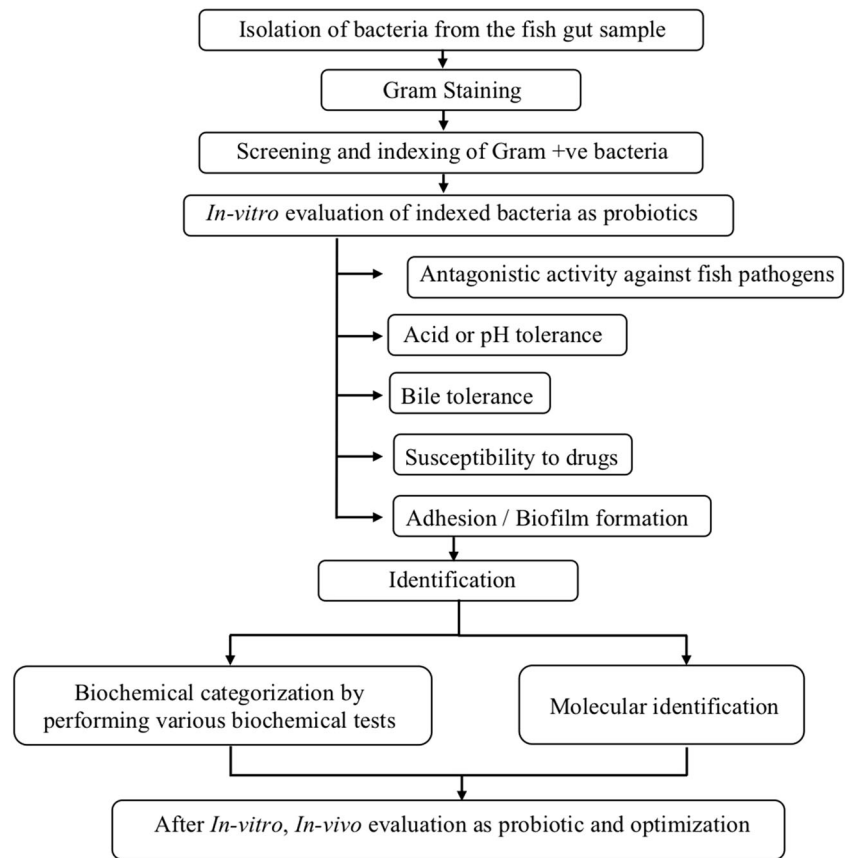
2 Selection criteria for probiotics

The main purpose of probiotics is to establish or to maintain a relationship between beneficial and harmful bacteria which is usually present in the intestine or gut of fish (Thirumurugan and Vignesh 2015; Olsson et al. 1992). Effective probiotics should possess certain qualities which are specified underneath: (Olsson et al. 1992; Merrifield et al. 2010; Pandya 2016; Gatesoupe 1999; Ouwehand et al. 1999a; Ouwehand et al. 1999b; Holzapfel and Schillinger 2002; Fuller 1989).

1. The probiotics should have a beneficial effect on the growth, development and protection of fish against various pathogenic bacteria.
2. The probiotic bacteria should not have any harmful effect on the host.
3. The probiotics should not have the ability of drug resistance, they should have the ability to keep up the hereditary traits.
4. For the utilization of probiotics as an efficient feed, they should exhibit following properties:
 - Acid and bile tolerance
 - Resistance to gastric juices
 - Adherence to digestive system surface
 - Antagonism towards pathogens
 - Stimulation of the immunity
 - Increase in the gut motility
 - Survival in mucous
 - Production of enzymes and vitamins
5. They should have good sensorial properties, fermentative action, tolerance towards freeze-drying and viability in feed during packaging and storing process.

Bacteria isolated from different sources are subjected to screening through multiple steps in order to assess their potential as ideal probiotics. The screening process involves gram staining, indexing, in-vitro evaluation of antagonistic properties, acid tolerance, bile tolerance, susceptibility to drugs and biofilm formation. Figure 1 shows the sequential screening process for the selection of isolated bacteria as probiotics. Successful fulfillment of all criteria qualify them as potential probiotic fit for use in the aquaculture.

Fig. 1 Schematic representation of the screening process for the selection of isolated bacteria as ideal probiotics



3 Probiotics & aquaculture

Usually the aquatic probiotics are commercially available in two major forms- dry and liquid. Dry forms have higher shelf life and are mixed with water or feed which is given to the host. On the other hand, the liquid form of probiotics, usually preferred in egg hatcheries is directly blended with the feed or added to the tanks (Decamp and Moriarty 2007). The liquid forms of probiotics are reported to show better and positive results due to their lower density than spore and dry form probiotics (Nageswara and Babu 2006).

The aquatic probiotics can be further categorized into two classes based on their mode of administration. First one involves the mixing of probiotic bacteria with feed supplement for the enhancement of useful bacteria inside the gut. Second class involves the addition of probiotic directly to the water so that they can consume nutrients available in the water and inhibit the proliferation of pathogens. These two categories of probiotics were used in finfish and shrimp aquaculture (Nageswara and Babu 2006; Sahu et al. 2008).

The probiotics isolated from different natural sources such as gastrointestinal tract (GIT), stomach, gill, kidney, gonads and other internal organs are called putative probiotics. In contrast, the commercial sources (non-putative) comprise of those which are already synthesized and commercially

available in the market. The most frequently used probiotic microorganisms belong to *Bacillus*, *Lactobacillus* and *Bifidobacterium* genus (Nwana 2015). Various species of *Lactobacillus*, *Bifidobacterium* and *Streptococcus* reported for use in aquaculture as probiotics, include *L. acidophilus*, *L. casei*, *L. fermentum*, *L. gasseri*, *L. plantarum*, *L. salivarius*, *L. rhamnosus*, *L. johnsonii*, *L. paracasei*, *L. reuteri*, *L. helveticus*, *L. bugarius*, *Bifidobacterium bifidum*, *Bifidobacterium breve*, *Bifidobacterium lactis*, *Bifidobacterium longum*, *Saccharomyces species*, *Saccharomyces boulardii*, *S. thermophiles* and *S. cremoris* (Nwana 2015).

Various aquatic probiotics have been reported which show activity not only against bacterial pathogen, but also against fungus and virus to improve growth and immunity of the host.

3.1 Antibacterial activity

Many probiotics used in aquaculture are well-known for their antibacterial property against known pathogens. *Lactococcus lactis* RQ516 probiotic shows inhibitory action against *Aeromonas hydrophila* when given to Tilapia (*Oreochromis niloticus*) (Zhou et al. 2010). Also *L. lactis* probiotic has antibacterial activity against two pathogens-*Yersinia ruckeri* and *Aeromonas salmonicida* that affects the fish growth (Balcazar et al. 2007a, b). *Leuconostoc mesenteroides* has

the potential to inhibit the fish pathogens found in Nile tilapia (*O. niloticus*) (Zapata and Lara-Flores 2012). According to reports, *Bacillus subtilis* considerably reduces the motile *Aeromonads*, total *Coliforms* and *Pseudomonads* found in ornamental fishes (Ghosh et al. 2008; Newaj-Fyzul and Austin 2015). Lactic acid bacteria such as *Lactobacillus acidophilus*, *Lactobacillus buchneri*, *Lactobacillus fermentum*, *Lactococcus lactis*, and *Sterptococcus salivarius* were isolated from Spanish mackerel (*Scomberomorus commerson*) intestine and were capable to inhibit the *Listeria innocua* growth (Moosavi-Nasab et al. 2014). Many *Lactobacilli* species isolated from the intestine of *Anguilla* species, *Clarias orientalis*, *Labeo rohita*, *Oreochromis* species and *Puntius carnaticus* showed significant antimicrobial activity against *Aeromonas* and *Vibrio* species (Dhanasekaran et al. 2008).

3.2 Antiviral activity

In recent years, the antiviral activity of probiotics has gained attention (Lakshmi et al. 2013), but the exact mechanism of action through which probiotic bacteria show antiviral effects is still unknown. However the in-vitro analysis reveals that the inhibition of viruses can occur by secretion of extracellular enzymes produced by the bacteria. For example, *Aeromonas* species, *Corynebacterium*, *Pseudomonas* and *Vibrio* species show the antiviral activity against the IHNV (Infectious hematopoietic necrosis virus) (Kamei et al. 1988; Zorriehzahra et al. 2016). Feeding of probiotic strain *Bacillus megaterium* has increased the resistance against WSSV (white-spot syndrome virus) in the shrimp, *Litopenaeus vannamei* (Li et al. 2009). The research has reported that probiotics strains *Bacillus* and *Vibrio* species are effective against WSSV and efficiently protect *Litopenaeus vannamei* (Balcazar 2003). Application of *Lactobacillus* as probiotic, either as a single strain or as a mixture with Sporolac resulted in better resistance against lymphocystis viral disease which is found in *Paralichthys olivaceus* (olive flounder) (Harikrishnan et al. 2010).

3.3 Antifungal activity

Only few studies have been reported about the antifungal activity of probiotics. *Aeromonas* strain A199 from *Anguilla australis* (eel) culture water, had high inhibitory property against *Saprolegnia* species (Lategan et al. 2004). In another study, *Pseudomonas* species M162, *Pseudomonas* species M174 and *Janthinobacterium* species M169 have increased the immunity against saprolegniasis in *Oncorhynchus mykiss* (rainbow trout) (Zorriehzahra et al. 2016). In 2012, Nurhajati et al. demonstrated that *Lactobacillus plantarum* FNCC 226 showed inhibitory potential in catfish (*Pangasius hypophthalmus*) against *Saprolegnia parasitica* A3 (Nurhajati et al. 2012).

The reported probiotic strains used in aquaculture can either be obtained commercially or isolated from different fish species. A detailed summary of different probiotics, their sources and the beneficial effects on the host are given in Table 1.

4 Mode of action

Probiotics have a special mode of action to protect the host from intestinal issues. The probiotic microorganisms hinder the establishment of different pathogenic bacteria by a process called colonization resistance. Probiotic microorganisms secrete a variety of inhibitory substances which inhibit Gram +ve and Gram -ve microscopic organisms. Principally, these inhibitory secretions are acetic acid, lactic acid, H₂O₂, bacteriocins and so on. These secretions decrease the number of pathogens by inhibiting the formation of virulence substances (Nwanna 2015). Oelschlaeger (2010) explained the mode of action of probiotics in a simple way in which probiotics modulate the acquired immune system as well as innate immunity to prevent host gut from disease causing pathogens and to treat against various digestive tract inflammations. Next possible action is that, they directly affect the pathogenic bacteria present in the gut, thus, resulting in the restoration of the probiotics in the gut. Finally they target various toxins produced by the microbial population resulting in their detoxification and inactivation in the gut (Oelschlaeger 2010). Thus, all modes of action of probiotics are directly associated with gut microbiota (Wolf 2006; Pandiyan et al. 2013). Probiotic secrete antagonistic compounds which help to improve the immunity and enhance the growth of fish. It also helps to improve the water and soil quality. The mode of action of probiotics is shown in Fig. 2.

Some possible well-known mechanisms by which probiotic bacteria protect the host organism against intestinal disorders are as follows:

4.1 Competition for space / blocking of adhesion sites

The activity of probiotics is visualized by the aggressive hindrance for the attachment sites on intestinal epithelial layer (Nwanna 2015). The mechanism of action by which probiotic bacteria struggle for the adhesion site is called 'competitive inhibition'. The ability of bacteria to colonize the gut and adhere to the epithelial surface and subsequently inhibit the adhesion of pathogens is desirable criteria in the selection of probiotics (Balcazar et al. 2006a, b; Lazado et al. 2011). *Lactobacillus* prevent the adhesion of the pathogenic bacteria such as *Escherichia coli*, *Klebsiella* species and *Pseudomonas aeruginosa* on intestinal cells of the host (Nwanna 2015).

Table 1 Probiotic species used in aquaculture, source and beneficial effects to the host species

Probiotic species	Source of probiotics	Beneficial effects	References
<i>Lactobacillus acidophilus</i> <i>Streptococcus faecium</i>	Commercial (All Tech, Nicholasville, KY)	Best growth performance and feed efficiency	Lara-Flores et al. (2003)
<i>Bacillus subtilis</i> <i>Lactobacillus acidophilus</i>	Commercial	Enhanced the non-specific immune parameters and enhance the challenge against <i>Edwardsiella tarda</i> infection	Tovar-Ramirez et al. (2004)
<i>Bacillus cereus</i> <i>Paenibacillus polymyxa</i>	Seawater, sediment and gut of healthy fish (<i>Lates calcarifer</i>)	Improved resistance against pathogenic <i>Vibrio</i> spp.	Ravi et al. (2007)
<i>Lactococcus lactis</i> CLFP 101 <i>Lactobacillus plantarum</i> CLFP 238 <i>Lactobacillus fermentum</i> CLFP 242	<i>Oncorhynchus mykiss</i> (Rainbow trout)	Reduce the adhesion of pathogens i.e. <i>Aeromonas salmonicida</i> , <i>Aeromonas hydrophila</i> , <i>Yersinia ruckeri</i> and <i>Vibrio anguillarum</i> to intestinal mucus and shows antibacterial activity against these fish pathogens.	Balcazar et al. (2008)
<i>Lactobacillus plantarum</i> <i>Bacillus subtilis</i>	<i>Labeo rohita</i>	Shows antagonistic activity against <i>Aeromonas hydrophila</i>	Giri et al. (2011)
<i>Bacillus coagulans</i> <i>Bacillus mesentericus</i> <i>Bifidobacterium infantis</i>	<i>Puntius conchoni</i>	Probiotic bacteria significantly established in gut of <i>P. conchoni</i> and significant effects on the pathogenic gut inhabitants of the fish.	Divya et al. (2012)
<i>Bacillus subtilis</i>	<i>Cyprinus carpio</i> (Common carp)	Inhibit the growth of <i>Aeromonas hydrophila</i>	Al-Faragi and Alsaphar (2012)
<i>Bacillus subtilis</i>	<i>Cyprinus carpio</i> (Common carp)	Growth promoting probiotic, enhance growth at the rate of 4×10^8 cells per 100 g of feed. Shows better growth, feed conversion ratio (FCR), specific growth rate (SGR) and feed conversion efficiency (FCE)	Bisht et al. (2012)
<i>Nitrosomonas species</i> <i>Nitrobacter species</i>	Commercial	Improves water quality and lowers the pathogenic (<i>Pseudomonas</i> species) bacterial loads in fish ponds.	Padmavathi et al. (2012)
<i>Lactococcus lactis</i> (D1813)	<i>Marsupenaeus japonicas</i>	Exhibit highest amount of IFN- γ production and bactericidal activity. Inhibit the infection caused by <i>Vibrio penaeicida</i> .	Maeda et al. (2014)
<i>Enterobacter</i> sp. strain C6–6	<i>Oncorhynchus mykiss</i> (Rainbow trout)	Protects the fish against <i>Flavobacterium psychrophilum</i> infection, reduce the mortality and enhance the immunity of fish.	LaPatra et al. (2014)
<i>Bacillus subtilis</i>	<i>Macrobrachium rosenbergii</i>	Increase in the growth, survival, improve food digestion, reduce the mortality caused by pathogenic bacteria (<i>Aeromonas hydrophila</i>)	Ramzani et al. (2014)
<i>Bacillus cereus</i>	<i>Cirrhinus mrigala</i>	Shows high growth performance like specific growth rate, body weight and also shows inhibition against the pathogenic strain (<i>Aeromonas hydrophila</i>)	Bhatnagar and Lamba (2015)
<i>Bacillus subtilis</i> <i>Bacillus aerophilus</i> <i>Bacillus firmus</i>	<i>Labeo rohita</i>	Improves digestion and fight against the fish pathogens such as <i>Providencia rettgeri</i> and <i>Aeromonas</i> species.	Thankappan et al. (2015)
<i>Lactococcus lactis</i> <i>Lactobacillus plantarum</i>	Bean sprouts <i>Paralichthys olivaceus</i>	Show improve phagocytic activity of innate immune cells, skin mucus lysozyme activity and improves host innate immunity, weight gain and survival rate following <i>Streptococcus iniae</i> challenge.	Beck et al. (2015)
<i>Bacillus subtilis</i> <i>Pediococcus acidilactici</i> <i>Enterococcus faecium</i> <i>Lactobacillus reuteri</i>	Commercial	Increase growth performance, health status and also modulate intestinal microbial community.	Giannenas et al. (2015)
<i>Bacillus subtilis</i> <i>Lactococcus lactis</i> <i>Saccharomyces cerevisiae</i>	<i>Labeo rohita</i>	Strains are more efficient in converting organic matter, adhere to the intestine, enhance the growth and survival of <i>L. rohita</i> .	Abareethan and Amsath (2015)
<i>Bacillus licheniformis</i>	Commercial	Increase the growth, immune response and disease resistance of juvenile tilapia against <i>Streptococcus iniae</i> .	Han et al. (2015)

Table 1 (continued)

Probiotic species	Source of probiotics	Beneficial effects	References
<i>Bacillus pumilus</i>	<i>Labeo rohita</i>	<i>Bacillus pumilus</i> treated fish show maximum percentage of total erythrocyte count, haemoglobin concentration and haematocrit concentrations which improves survival and therefore establish better health conditions.	Rajikkannu et al. (2015)
<i>Bacillus pumilus</i> <i>Bacillus mojavensis</i>	<i>Oratosquilla oratoria</i> <i>Portunus trituberculatus</i>	Shows antagonism against <i>Vibrio parahaemolyticus</i>	Liu et al. (2015)
<i>Lactobacillus gasseri</i> TSU3 <i>Lactobacillus animalis</i> TSU4	<i>Catla catla</i>	Capable of adhering to epithelial cells and mucosal surfaces and exhibit strong anti-bacterial activity against all pathogens including <i>Aeromonas hydrophila</i> .	Sahoo et al. (2015)
<i>Pseudomonas psychrotolerans</i> <i>Vibrio ichthyenteri</i> <i>Labrenzia sp.</i>	<i>Sparus aurata</i>	Enhance the immune defence of fish. Show antagonism against three fish pathogens: <i>Vibrio anguillarum</i> , <i>Photobacterium damsela</i> and <i>Pseudomonas anguilliseptica</i> .	Mancuso et al. (2015)
<i>Bacillus amyloliquefaciens</i> (KF623290) <i>Bacillus sonorensis</i> (KF623291)	<i>Cirrhinus mrigala</i>	Shows antagonistic activity against <i>Pseudomonas putida</i> and <i>Aeromonas salmonicida</i> .	Dutta and Ghosh (2015)
<i>Lactobacillus plantarum</i>	Sediments	Stimulates growth rate, feed efficiency, conferred the best performance and immune response of Nile tilapia challenged with <i>Aeromonas hydrophila</i> .	Hamdan et al. (2016)
<i>Bacillus stratosphericus</i> (KM277362) <i>Bacillus aerophilus</i> (KM277363) <i>Bacillus licheniformis</i> (KM277364) <i>Solibacillus silvestris</i> (KM277365)	<i>Cirrhinus mrigala</i>	Strains grow better in intestinal mucus and produce various cellular components which exhibit bactericidal activity against the fish pathogens.	Mukherjee et al. (2016)
<i>Lactobacillus plantarum</i>	Shellfish	Show inhibitory activity against pathogens including <i>S. aureus</i> , <i>S. typhimurium</i> , <i>S. enteritidis</i> , <i>E. coli</i> O157:H7, <i>V. ichthyenteri</i> , <i>S. iniae</i> , and <i>V. parahaemolyticus</i> .	Kang et al. (2016)
<i>Lactobacillus sp.</i> <i>Lactococcus sp.</i>	<i>Alestes baremoze</i>	Suppress the pathogenic bacteria, <i>S. aureus</i> , <i>Streptococcus sp.</i> , <i>Proteus sp.</i> , <i>Pseudomonas sp.</i> and <i>E. coli</i> .	Kato et al. (2016)
<i>Bacillus amyloliquefaciens</i>	<i>Clupanodon punctatus</i> <i>Epinephelus coioides</i>	Improve the growth performance, enhance the immune parameters in turbot and also fight against <i>V. anguillarum</i> infection.	Chen et al. (2016)
<i>Kocuria sp.</i> <i>Rhodococcus sp.</i>	<i>Oncorhynchus mykiss</i> (Rainbow trout)	Produce extracellular enzymes (secondary metabolites) which is inhibitory to <i>Virbio anguillarum</i> , <i>V. ordalii</i> , <i>E. coli</i> , <i>Pseudomonas aeruginosa</i> and <i>Staphylococcus aureus</i> .	Sharifuzzaman et al. (2017)
<i>Enterococcus hirae</i>	<i>Catla catla</i>	Persist in simulated gastric conditions with the inhibition capability of various pathogens like <i>Staphylococcus aureus</i> (MTCC 3160), <i>Escherichia coli</i> (MTCC 40), <i>Pseudomonas aeruginosa</i> (MTCC 424) and <i>Salmonella typhi</i> (MTCC 3215).	Adnan et al. (2017)
<i>Bacillus pumilus</i> AQAHBS01	<i>Oreochromis niloticus</i>	Improves immunity of Nile tilapia and enhance disease resistance against <i>Streptococcus agalactiae</i> .	Srisapoom and Areechon (2017)
<i>Lactobacillus farraginis</i> <i>Pediococcus acidilactici</i> <i>Pediococcus pentosaceus</i> <i>Bacillus sp.</i>	<i>Salmo salar</i> (Atlantic salmon) <i>Mystus vittatus</i>	Produce antimicrobial compounds against fish pathogens, have good colonization capacity on gastrointestinal tract of salmon.	Amin et al. (2017) Nandi et al. (2017)

Table 1 (continued)

Probiotic species	Source of probiotics	Beneficial effects	References
<i>Bacillus subtilis</i>	<i>Labeo rohita</i>	Shows antibacterial activity against four fish pathogens, <i>Aeromonas salmonicida</i> , <i>A. hydrophila</i> , <i>A. sobria</i> and <i>Pseudomonas fluorescens</i>	Banerjee et al. (2017)
<i>Bacillus subtilis</i> HAINUP40	Pond water	Show inhibitory activity against four fish pathogens such as <i>Aeromonas hydrophila</i> , <i>Aeromonas salmonicida</i> , <i>Bacillus mycoides</i> and <i>Pseudomonas fluorescens</i> .	
<i>Bacillus subtilis</i>		Enhance growth performance, immune response and disease resistance of Nile tilapia against <i>Streptococcus agalactiae</i> .	Liu et al. (2017)
<i>Bacillus licheniformis</i>	Shrimp	Enhance non-specific immune responses, growth performance and disease resistance against <i>A. salmonicida</i> in juvenile rainbow trout.	Park et al. (2017)

Probiotic adhesion can be non-specific due to the presence of physiochemical agents or specific due to the adhesion of the probiotics either on the surface of adherent bacteria or the receptor molecules on the epithelial cells (Salminen et al. 1996; Lazado et al. 2015).

4.2 Production of inhibitory substances

The probiotic bacteria produce inhibitory substances which have bacteriostatic or bactericidal influences on pathogenic microbes (Servin 2004) like hydrogen peroxide, bacteriocins,

lysozymes, siderophores, proteases, and many others (Panigrahi and Azad 2007; Tinh et al. 2008). Some bacteria produce volatile fatty acid (acetic, butyric, lactic and propionic acid) and organic acid, as a result of which there is a decrease in pH of gastrointestinal tract. Hence, it inhibits the proliferation of opportunistic pathogens (Tinh et al. 2008). A compound named indole (2,3-benzopyrrole) has inhibitory potential against various pathogens i.e. *Vibrio anguillarum*, *Aeromonas salmonicida*, *Edwardsiella tarda* and *Yersinia ruckeri* (Gibson 1998; Lategan et al. 2006; Abbass et al. 2010).

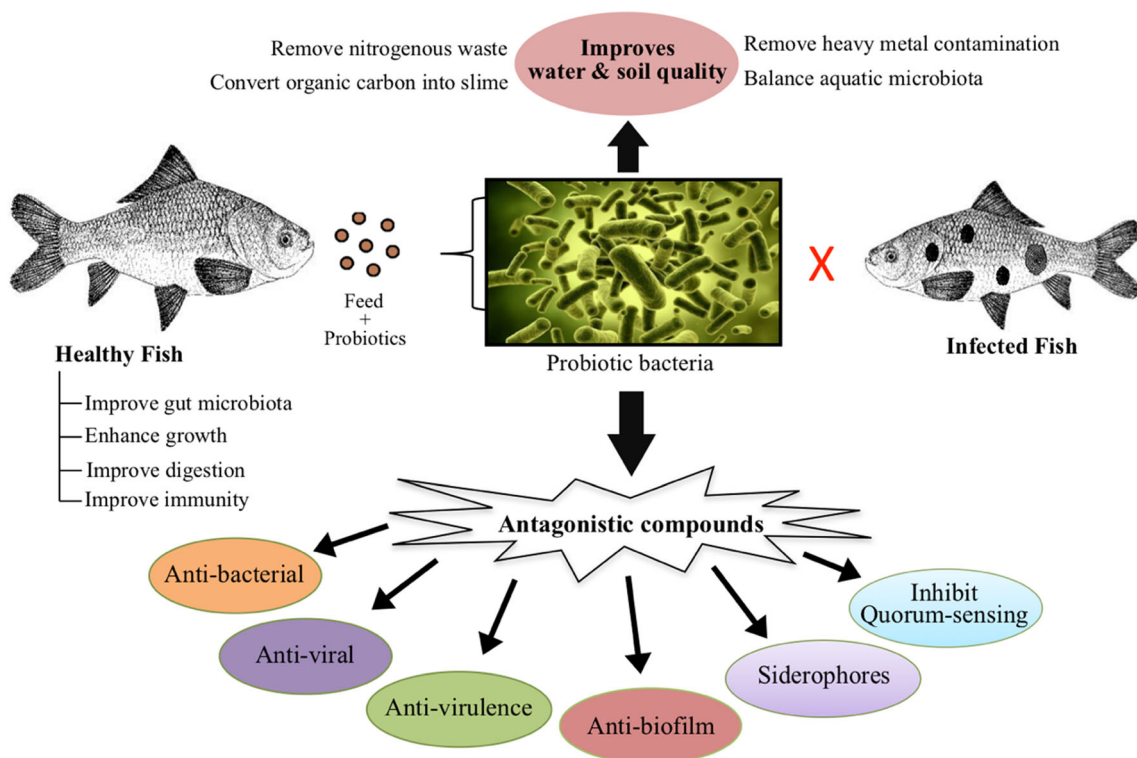


Fig. 2 Mode of action of probiotics. Modified from Chauhan and Singh (2018)

4.3 Competition for nutrients

The survival of any microbial population depends on its ability to compete for nutrients and available energy with other microbes in the same environment (Verschuere et al. 2000). While struggling for nutrients, probiotics can out-contend the pathogens by utilizing all the available nutrients that would have been consumed by pathogenic microorganisms. This mechanism would restrict the pathogen's presence in the intestinal tract because without nutrients the bacteria cannot survive (Nwanna 2015). For example, siderophores are low-molecular-weight iron-chelating agents that dissolve precipitated iron or extract it from the iron complexes, thus making it available for bacterial growth (Neilands 1981). Siderophore-producing bacteria can be used as probiotics because they can sequester ferric iron in an iron-low environment, hence, making it unavailable for the growth of pathogenic bacteria (Tinh et al. 2008). A culture supernatant of *Pseudomonas fluorescens* which was grown in iron-limited conditions inhibits the growth of *Vibrio anguillarum*. It has been shown that *P. fluorescens* can competitively inhibit the growth of fish pathogen *Aeromonas salmonicida* by competing for the available free iron (Gram et al. 1999; Smith and Davey 1993).

4.4 Improving water quality

According to the studies, use of Gram +ve bacteria (*Bacillus* species) as probiotics to improve the water quality has been reported. It was concluded that the Gram positive bacteria, especially *Bacillus* species are more efficient in conversion of organic matter into CO₂, slime or bacterial biomass. The studies suggest better performance of Gram positive bacteria over Gram negative bacteria. It is also suggested that the farmers can control the accumulation of dissolved and particulate organic carbon during the growing season by maintaining high level of probiotics in the production pond (Balcazar et al. 2006a, b; Mohapatra et al. 2013). The probiotic bacteria possess significant algicidal activity and affects several species of microalgae (Fukami et al. 1997). The nitrifying probiotic bacteria are beneficial as they increase the number of microbial species in water and improve the water quality by eliminating ammonia and nitrate toxicity (Zorriehzahra et al. 2016; Mohapatra et al. 2013). Also, after the use of probiotics, other parameters like temperature, pH, dissolved oxygen, ammonia and hydrogen sulfide in rearing water were found to be of better quality. Thus, probiotics maintain a positive and healthy environment for shrimp and prawn larval culture in aquatic system (Aguirre-Guzman et al. 2012; Banerjee et al. 2010).

4.5 Disruption of quorum sensing

Quorum Sensing (QS) is a bacterial regulatory mechanism, which is responsible to control the expression of various biological macromolecules such as, the virulence factors in a cell density-dependent manner. In this mechanism, bacteria regulate the gene expressions by producing, releasing and recognizing small signal molecules called auto-inducers (Chu et al. 2014). Many bacteria are using this system to communicate and regulate a diverse array of physiological activities (Miller and Bassler 2001). Disruption of the QS system of pathogens has been proposed as a new anti-infective strategy in aquaculture (Defoirdt et al. 2004; Zorriehzahra et al. 2016).

Since N-Acyl homoserine lactones (AHLs) are the main family of QS auto-inducers used in Gram negative bacteria, their Biodegradation prove to be an efficient way to interrupt QS. *Bacillus* sp. QSI-1 is an efficient quorum quencher on virulence factors production and biofilm formation of fish pathogen *Aeromonas hydrophila* (Chu et al. 2014). *Bacillus* sp. QSI-1 reduced the accumulation of AHLs but did not affect the growth of *A. hydrophila* YJ-1. It has been found that the supernatant of QSI-1 showed significant inhibition of protease production (83.9%), hemolytic activity (77.6%) and biofilm formation (77.3%) in YJ-1. In biocontrol experiment, QSI-1 significantly reduced the pathogenicity of *A. hydrophila* strain YJ-1 in zebrafish (*Danio rerio*). The fish fed with QSI-1 were observed to have a relative percentage survival of 80.8%. The results indicated that AHLs degrading bacteria should be considered as an alternative for antibiotics in aquaculture for the bio-control of bacterial fish diseases (Chu et al. 2014). Probiotic bacteria such as *Lactobacillus*, *Bifidobacterium* and *Bacillus cereus* strains degrade the signal molecules of pathogenic bacteria by enzymatic secretion or production of auto-inducer antagonists (Brown 2011). Medellin-Pena et al. (2007) showed that *Lactobacillus acidophilus* secretes a molecule that inhibits the QS or interacts with bacterial transcription of *Escherichia coli* O157 gene.

5 Methods of administration of probiotics

Various methods have been put forth to regulate the use of probiotics in aquaculture. They can be added in feed, resulting in the colonization on the surface of intestinal tract. In prawns, the most common regulatory method for administration of probiotics is through water/oral routine (Huang et al. 2006). But most of the probiotics are designed in such a way that they can be mixed with the feed additives to show high efficiency against pathogens (Austin et al. 1992; Gildberg and Mikkelsen 1998; Hai et al. 2009; Gomes et al. 2009). The probiotics such as *Lactobacillus rhamnosus* were reported to improve the fecundity of *Danio rerio* (Gioacchini et al. 2010). Other methods such as addition of probiotics directly into

water or in bacterial suspension were also reported (Queiroz and Boyd 1998; Gibson et al. 1998; Ringo and Vadstein 1998; Cha et al. 2013; Hansen and Olafsen 1989; Sung et al. 1994; Itami et al. 1998).

Probiotics can be used individually or in a combination of different strains (Havenaar et al. 1992; Salinas et al. 2005; Kesarcodi-Watson et al. 2008; Kesarcodi-Watson et al. 2012). Previous reviews on probiotics have focused on the utilization of sole culture species, and it is speculative whether combination two or more cultures of probiotic strains would be useful. Mixed probiotic strains are more efficient than probiotics based on a single strain (Verschuere et al. 2000; Hai et al. 2009). Multi-species and multi-strain probiotics enhance the defense mechanism against various infectious diseases (Kesarcodi-Watson et al. 2012; Timmerman et al. 2004). A recent study compared the activity of mixed strain of *Lactobacillus acidophilus* and *B. subtilis* in Nile tilapia in which serum bactericidal activity and hematocrit values were higher in comparison to sole strain (Aly et al. 2008a, b). Similar studies were conducted to modulate immunity against *Streptococcus iniae* by a mixture of *Lactobacillus plantarum* and *Lactococcus lactis* in Japanese flounder (Beck et al. 2015). In the growth and survival of *Labeo rohita*, multi strain probiotics have been efficiently used which enhanced fry and hatchling stages (Jha et al. 2015).

Synbiotics is the combination of probiotics with various plant products and prebiotics (Salminen et al. 1998; Van Hai and Fotedar 2009). It has been reported in many studies that synbiotics improves the microbial supplementation in the gastrointestinal tract of the host organism (Gibson and Roberfroid 1995). The feeding of synbiotic *Enterococcus faecalis* and mannan-oligosaccharide (MOS) showed better FCR (food conversion ratio) as compared to feeding of probiotic and prebiotic individually (Rodriguez-Estrada et al. 2009). The application of probiotics, prebiotics and synbiotics have improved the survival of aquatic organisms against pathogenic bacteria. The survivability were found to be maximum in the probiotic treatment followed by prebiotic and synbiotic (Daniels et al. 2013; Decamp and Moriarty 2007).

The enrichment of live feed with probiotics as encapsulation has developed into an interesting idea. In this technique, the probiotic bacteria can remain viable or even proliferate on the live feed. Therefore, probiotics can be delivered by the live feed to the host in a very efficient manner (Hai 2015). Various live feeds have been reported so far such as copepods (Sun et al. 2013), rotifer (Gatesoupe 1997) and *Artemia* species (Daniels et al. 2013; Gatesoupe 1994; Van Hai et al. 2010), in which probiotics were encapsulated. This approach of enrichment of live feed with probiotics has proved to be effective over other conventional methods. Van Hai et al. 2010 have reported an effective enrichment of *Artemia nauplii* using a combination of *Pseudomonas synxantha* and *Pseudomonas aeruginosa* for *Penaeus latissulcatus* (western king prawn).

Similarly, Sun et al. 2013 have reported that the copepod (*Pseudodiaptomus annandalei*) is an appropriate vector of probiotic (*Bacillus* species) as live feed for *Epinephelus coioides* larvae.

The probiotics can be administered in either form- as live or dead strains. Various reports are available for the use of probiotics in either form. The comparison of live and dead forms reveals an interesting observation. Live probiotics provide immunity to the host in most of the cases and in a few cases certain inactivated probiotics also do the same. Hence, the use of probiotics in live or heat killed forms are case specific and cannot be generalized. For instance, Sharifuzzaman et al. 2011; Arijo et al. 2008; Panigrahi et al. 2011; Ramesh et al. 2015 have reported the use of viable probiotics with better results. Sharifuzzaman and Austin 2010; Arijo et al. 2008 have demonstrated the role of live probiotic cells Kocuria SM1 by production of cross-reactive antibodies in rainbow trout to protect against infections due to *Vibrio anguillarum*, *V. ordalii* and *V. harveyi*. Similarly, live cells of *Bacillus licheniformis* and *Bacillus pumilus* exhibited an enhanced expression of lysozyme activity and respiratory burst in rohu species (Ramesh et al. 2015). Panigrahi et al. 2011 states that higher expression of immune genes (TNF, TGF- β , IFN and Ig) is responsible for better immunity. The expression of these immune genes is induced using live probiotic cells (live-spray and freeze-dried) compared to the heat-killed ones. The phagocytic activity was found to be higher in rainbow trout, when they were fed with live cells of probiotic bacteria *Lactobacillus rhamnosus* JCM1136 as compared to heat-killed cells (Panigrahi et al. 2005).

Also, in some cases the supplementation of cell-free supernatant and heat-killed probiotics stimulated innate immunity of the fish (Irianto and Austin 2003). But they offer poor protection to rainbow trout and Chinese drum (*Miichthys miiuy*) against pathogens, *V. anguillarum*, *Streptococcus iniae*, *Aeromonas hydrophila* and *Lactococcus garvieae* (Brunt and Austin 2005; Pan et al. 2008). When Nile tilapia was nourished with both dead and live probiotics against *Edwardsiella tarda* disease, dead probiotics were found ineffective as compared to viable probiotics (Taoka et al. 2006).

The administration duration of probiotic bacteria is also considered a very significant factor. According to research, the time-period for application of the potential probiotic can be as short as 6 days or as long as 5 months or even 8 months (Joborn et al. 1997; Aubin et al. 2005; Aly et al. 2008a, b). Prolonged administration of probiotics can induce immune-suppression of continuous responses of nonspecific immune systems (Sakai 1999). Supplementation of probiotic bacteria has demonstrated to give short-term benefits. However, they were not detected inside the gastrointestinal tract over a period of 1–3 weeks (Robertson et al. 2000; Kim and Austin 2006; Balcazar et al. 2007a, b). Short-term supplementation has turned out to be effective, while the data on long-term effectiveness is not

available (Brunt et al. 2007; Newaj-Fyzul et al. 2007; Pieters et al. 2008; Wu et al. 2015; Skjermo et al. 2015). Feeding of probiotics (*Shewanella xiamenensis* and *Aeromonas veronii*) to grass carp for about 28 days reduced the cumulative mortality when challenged with *Aeromonas hydrophila* (Wu et al. 2015). Aubin et al. 2005 checked the recovered amount of probiotics over a time period and observed that recovery levels were found to be higher after 20 days than 5 months. The frequency of administration of probiotics also play a very important role in maintaining the effectiveness and function of probiotics. A daily application of probiotics is better than thrice a week during the culture period (Guo et al. 2009).

6 Conclusion

In recent years, the use of probiotics as biological control agent has improved fish performance, water quality, prevention of diseases, enhancement of immune responses and so on. This review concludes that several probiotic strains are highly specific while others are quite selective. Efforts need to be made to streamline the whole range of probiotic strains and categorize them based on their action-specific mechanism. A simple step in this direction is going to make the use of probiotics very efficient, economical and eco-friendly. After proving the worth of probiotics, there is a need to look forward towards designing probiotic strains which are specific and can be used to target specific fish species. The evaluation of optimal conditions for probiotic interaction with the host also holds a lot of scope for further investigation. In the past, there have been instances of failure of in-vivo studies which were conducted based on the positive in-vitro results. We need to detail out the conditions in real samples which may affect their survival, colonization, proliferation and interaction with the host in a particular environment. This will help us to properly screen and test probiotics which will lead to no mismatch in in-vitro and in-vivo observations. Other important scope for future research is to study the fate of probiotics in host organism. The fate of live strains and durability of health effects of probiotics in host organism are uncertain and require further investigation.

After doing much study about the efficacy and action mechanism of probiotics, there are still many doubts which are unclear. Nevertheless, the future should focus on relevant research to develop innovative and suitable approach for administration of probiotic strains in foods and animals. Probiotic strains viability, functionality, host-microbe's interactions, antioxidant status, antagonistic and synergistic activity or probably side effects of probiotics should be the major concerns of study. In addition, advanced molecular level research is required on probiotic science for a better understanding of the molecular mechanisms and to decode the probiotic unique gene with novel applications.

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