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ENZYME-PRODUCING GUT BACTERIA OF FISH AND ITS EFFECT ON FISH HEALTH: A REVIEW

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AUTHORS' CONTRIBUTIONS

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

ABSTRACT

Like all multicellular organisms fish also lives in close association with microorganisms. They live in a symbiotic relationship and the bacteria provide protection, immunity and metabolic strength to the host and in return, the host gives nutrient-enriched media to it. Gut microbes of fish secret amylase, lipase, cellulase, protease, chitinase etc. and they play a significant role in digestion. To date, most of the studies on gut microbiota have emphasized the mammal. Contrary to this, information about the host-microbe interactions in fishes is limited. Therefore, a better understanding of this topic is the need of the hour. Exogenous enzymes can be produced by the gut microbes such as *Lactobacillus* spp., *Pseudomonas* spp., and *Vibrio* spp. etc to improve the digestion of food and degradation of complex and large molecules, such as protein, starch, and chitin. Similarly, when the composition of microbiota changes many biosynthesis and metabolism pathways of carbohydrates, amino acids, and lipids also change. Epithelial absorption of fatty acid is facilitated by the colonization of the gut microorganisms, this colonization also protects the host against pathogenic bacteria. To achieve sustainable disease control and nutrient enhancement strategies in aquaculture practices an understanding of the dynamics and functions of the gut microbial community in fish is necessary as it will enable a more profound selection of the beneficial microorganisms.

Keywords: Enzymes; fish gut-bacteria; immunity; microbes; probiotics.

1. INTRODUCTION

Fishes are poikilothermic aquatic animals and they are considered as one of the best source of animal protein. They are rich in omega-3 fatty acids, vitamins like B2 and D and minerals such as iron, calcium, phosphorus, iodine, magnesium, zinc and potassium. During the last few decades, the consumption of fish has increased as the world population increased [1].

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Bacterial flora resides in the skin, intestine and various other organs of fishes [2]. Two types of bacteria are found inside the GI tract of fishes. One considered as transient (allochthonous), whereas the others mucus associated microflora (autochthonous) [3, 4]. The bacteria and host lives in symbiotic relationship as the host provide shelter to the microbe in return it helps the host with metabolic, protective and structural support [5–7]. Gut bacteria is also seen involved in feeding, metabolic processes, immune response and digestive processes of higher organisms as revealed in recent studies [6, 7]. In fish, bacteria from the gut provide enzymes like amylase, lipase, cellulase, protease, chitinase etc. and thus play a significant role in digestion[8]. Especially the major source of cellulase in animal body is bacteria. Life span, physiology, immunity, and barriers against the pathogen in fish can also be influenced by the gut bacteria [9].

Thus, gut bacteria can be termed as ‘extra organ’ as it plays an important role in physiology, intestinal as well as overall development of fish [10].

Various studies revealed that as fish grows it changes its feeding habit from omnivorous to carnivorous and thus changes its gut microbial content. Therefore it can be considered that the microbial diversity inside fish gut depends upon its age, diet, habitat, sex, stress etc. [11].

Several researchers such as [12-14] etc. reviewed the traditional method of absorption and digestion but these are not focused on gut bacteria-mediated digestion. Though few researches are available on enzyme producing gut bacteria of fishes they are mainly focused on one type of enzyme. Therefore, a compiled database of a few significant enzymes produced by the gut bacteria of fishes and their benefit in fish health is necessary.

The microbial community reside inside fish body also act in disease resistance. *B. thuringiensis*, SS4 isolated from fish gut showed that it has high protease activity which makes it potential for using in medicine and food industries [15]. Similarly in a study on Blue morph fish e *Lactobacillus acidophilus* showed highest pathogen resistance among 4 different strains isolated [16]. Therefore, a cost-effective evaluation of bacteria with beneficial functions is needed [17, 18]. This review will provide an understanding of beneficial fish gut bacteria which help to improve its nutrition and health. It may also help in developing a practical strategy to engineer indigenous fish bacteria for enhancing fish health, immunity, nutrition and disease control. Rather than single microbial species, microbial consortia are considered to be associated with health [19]. Microbial consortia became popular in influencing the early growth and development of eukaryotic hosts [20]. Therefore, a compiled review is needed in which we can get an idea of beneficial miocrobes reside inside fish gut. Hence, this review will help in choosing bacterial strains for combination to make a beneficial bacterial consortium.

In the GI tract of herbivorous, carnivorous and omnivorous fish species various studies have reported numerous microbial communities [3, 4, 21–28, 29–36]. However, surprisingly, in the case of herbivorous fish, the endosymbiotic community and its health benefits are poorly investigated. [37-39] in their reviews only mentioned about these but there was no such broad information. Though [24, 40, 41 and 36] presented little information on studies of exogenous enzyme activity in fish, a more precise and comprehensive review is needed it was evident that the GI tract of fishes possesses a wide range of microbiota producing enzymes like Cellulase, Protease, Lipase, Amylase, Chitinase (Tables 1-5). Furthermore, the role of enzyme-producing fish gut bacteria as probiotics in the enhancement of food digestibility and their effect on gut enzyme activity has been evaluated through several investigations (Tables 7-8).

In the present review, analysis of beneficial bacteria from the fish gut is addressed. The results cited include works published in renowned as well as minimally circulated and highly-priced journals so that people can access huge data at a low cost and time. This is performed to indicate that there are numerous interesting investigations published on the topic of enzyme-producing microorganisms isolated from the digestive tracts of fish.

2. CELLULASE-PRODUCING GUT BACTERIA OF FISH

Cellulase is an enzyme that converts or breaks polysaccharides into glucose or disaccharides. Shcherbina and Kazlauskiene (1971) first studied the presence of microbial cellulase in the distal intestine of common carp [42]. It has been proven that the primary source of cellulose in the gut of fish is microbiota; in the digestive tract of 42 different species they displayed cellulase activity and they suggested that microbiotas are a stable source of cellulolytic activity in these fishes [43]. Fishes utilizing cellulose and similar fibrous carbohydrates as cellulase activity has been reported in several fish species [44]. Symbiotic associations with microorganisms are required in the GI tract of many celluloses eating animals to digest cellulose and make the energy [45, 46]. Saha and Ray (1998) reported cellulase-producing bacteria in the gut of fishes but they didn't characterize it [47]. Further, the presence of cellulolytic bacteria has been documented in the GI tract of wood-eating catfishes, common carp and silver carp (*Hypophthalmichthys molitrix*) [30], rohu [47–50], murrel [49], grass carp [30, 51, 52], tilapia[51], catla and mrigal [50] and bata [50, 53]. From the proximal and distal intestine of three major carp isolated cellulase-producing autochthonous bacteria and the 16S rRNA gene sequence the most promising strains were analysed [54]. Further, 16S rRNA method was used to identify important cellulase-producing bacteria from the gut of grass carp and found that all of them belong to *Aeromonas* [55]. Generally, the presence of cellulolytic bacteria in the gut of carnivorous fish is more limited than the activity of cellulolytic bacteria in herbivorous fishes [56]. From the GI tract of marine fishes namely *Carangoides praeustus*, *Filimanus similis*, *Sardinella longiceps* and *Sillago sihama* four cellulolytic species of symbiotic bacteria were isolated [57].

From the Table 1 analysis, it can be drawn that fishes don't usually produce cellulase enzyme, it is mainly provided by the gut bacteria. The herbivorous fishes produce more cellulase enzymes as they consume plant material. The most common strain that produces cellulase in fish is *Bacillus.* Therefore, the introduction of cellulase to fish food might positively affect growth, feed utilization and nutrient digestibility, potentially reducing feed costs.

3. PROTEASE-PRODUCING BACTERIA IN FISH GUT

Protease is an enzyme that breaks proteins and peptides. It was studied that proteolytic enzyme activity increases considerably when common carp fry are administered with bovine trypsin in their diet [60]. Thus, Hamid et al. (1979) and Trust et al. (1979) first studied the occurrence of proteolytic bacteria in the gut of grey mullet and grass carp [61, 62]. One isolate from the intestinal contents of Arabesque greenling (*Pleurogrammus azonus*), showed strong proteolytic activity; however, the isolate was identified as genus Pseudomonas and displayed the highest protease production at 10 °C, but as the cultivation temperature increases the activity decreased [63]. In-vitro study on enzyme-producing gut bacteria of Rohu fingerling showed that *Bacillus circulans* Lr 1.1, *Bacillus pumilus* Lr 1.2 and *Bacillus cereus* Lr 2.2, are great producers of proteolytic enzymes in the hindgut region of detritivorous carp (*Labeo calbasu*) [48]. Carnivorous *Channa punctatus* showed higher proteolytic enzyme activity as compared to herbivorous *Labeo rohita* while experimenting with enumerated heterotrophic bacteria from the GI tracts [49]. Studies showed that strains isolated from the distal intestine of three species of Indian major carps showed the highest proteolytic activity [54]. Analysis of gut microbiota in *Labeo bata* revealed that higher amylase-producing bacteria are found in the foregut region, whereas the hindgut region exhibit higher cellulolytic and proteolytic enzyme-producing bacterial populations [50]. On screening of enzyme-producing autochthonous bacteria it was found that proteolytic activity was highest in *Heteropneustes fossilis* and bacteria found were mostly gram-positive and belong to *bacillus* sp. [64]. Armada and Simora (2016) obtained the highest protease activity at 25.32 ± 1.06 U/ mg protein and identified the strain as *Pseudomonas* spp. [65]. In a study on the gut bacteria of *Clarias batrachus* which is a carnivorous fish considerable amount of protease-producing bacteria were found in comparison to other enzyme-producing microbes [66]. In a study bacteria from freshly collected *Channa aurantimaculata* were found to be showing higher protease activity [11].

From the Table 2 analysis, it is evident that the protease-producing bacteria are majorly found in the hindgut region of fish. The carnivorous fishes show higher proteolytic activity than the herbivorous fish species and most of them belong to *Bacillus* and *Pseudomonas.* The proteolytic activity of these bacteria depends upon pH, temperature, and various environmental conditions.

Table 1. Cellulase-producing bacteria from GI tract of different fishes

Microorganisms	Isolated from	Reference
Bacillus circulans; B. pumilus; B. Cereus	*Labeo rohita*	[48]
Bacillus circulans, B. megaterium	*Oreochromis mossambica, Ctenopharyngodon idella*	[51]
Bacillus licheniformis; B. Subtilis	*Labeo bata*	[50]
Citrobacter sp.; *Enterobacter* sp.; *Bacillus coagulans*	Species of major Indian carp	[54]
Aeromonas sp.	*Ctenopharyngodon idella*	[55]
Bacillus subtilis, B. velesensis	*Piaractus esoiptamicus, Leporinus friderici.*	[58]

Bacillus thuringiensis, B. cereus, Bacillus sp	*Salmo salar*	[59]

Table 2. Protease-producing bacteria from the GI tract of different fishes

Microorganism	Isolated from	Reference
Enterobacter spp, *Vibrio* spp, *Pseudomonas* spp, *Acinetobacter* spp, *Aeromonas* spp.	*Mugil cephalus*	[61]
Strict anaerobes and Aeromonas hydrophila	*Ctenopharyngodon idella*	[62]
Vibrio spp.	*Centropristis striata*	[67]
Pseudomonas sp.	*Pleurogrammus azonus*	[63]
Flavobacterium balustinum	*Salmo salar*	[68]
Bacillus cereus; B. circulans; B. pumilus	*Labeo rohita*	[69]
Bacillus cereus	Nine different freshwater teleosts	[30]
Pseudoalteromonas spp	*Merluccius hubbsi*	[70]
Aeromonas spp, *Enterobacteriaceae, Pseudomonas* spp, *Flavobacterium* spp, *Micrococcus* spp	*Rutilus rutilus*	[71]
Bacillus cereus	*Mugil cephalus*	[72]
Citrobacter spp, *Enterobacter* spp, *Bacillus coagulans*	Three major Indian carp	[54]
Bacillus licheniformis, B. subtilis	*Labeo bata*	[50]
Bacillus thuringiensis, Bacillus cereus, Bacillus spp.	*Gadus morhua*	[73]

Table 3. Lipase-producing bacteria from the GI tract of different fishes

Microorganism	Isolated from	Reference
Strict anaerobes; *Aeromonas hydrophila*	*Ctenopharyngodon idella*	[62]
Agrobacterium; Pseudomonas; Brevibacterium; Microbacterium; Staphylococcus	*Salvelinus alpinus*	[40]
Vibrio spp., *Acinetobacter* spp. *Enterobacteriaceae, Pseodomonas* spp	*Dicentrarchus labrax* larvae	[67]
Vibrio spp.	*Salvelinus alpinus*	[76]
Bacillus thuringiensis, Bacillus cereus, Bacillus spp.	*Salmo salar*	[73]

4. LIPASE-PRODUCING BACTERIA IN FISH GUT

Lipase is a family of an enzyme that catalyses the breakdown of fats. In GI tracts the microbiota helps in the absorption efficiency of lipids. Bacterial strains isolated from the GI tract of grass carp show lipolytic activity which was strict anaerobes and *Aeromonas hydrophila* [62]. It has been proven that the *Vibrio* spp is one of the major strain showing lipase activity which was isolated from sea bass larvae, but 25% of the gut isolates showed lipase activity were classified as *Acinetobacter, Enterobacteriaceae* and *Pseudomonas* [67]. Lipase activity has been reported in the gut content or gut of most fish species studied, and it seems obvious if lipase activity is present then most of the intestinal lipase activity is located in the pyloric caeca and the proximal intestine [74]. In a study the maximum lipolytic activity was found in silver carp (*Hypophthalmichthys molitrix*) while investigating the gut bacteria of nine freshwater teleosts [30]. Mohan et al., (2012) also found that most of the lipase producing bacteria are belong to *Vibrio* spp. [75].

From this (Table 3) review, it can be drawn that most lipase-producing bacteria reside in the proximal portion of the gut. In the case of lipase activity, the dominant strains are *Vibrio* and *Bacillus*.

5. AMYLASE-PRODUCING BACTERIA IN FISH GUT

The enzyme amylase catalyses the hydrolysis of starch into sugar. Trust et al. (1979) first reported the occurrence of amylase-producing bacteria in the gut of grass carp (*Ctenopharyngodon idella*) [62]. In general, bacteria from the digestive tract of omnivorous fish show relatively higher amylase activity than that of carnivorous fish [77, 78], but dietary manipulation also affects its activity [77-80]. Das and Tripathi (1991) demonstrate the presence of amylase producing bacteria in the gut of various fishes but they did not characterize them [81]. *Vibrio* spp. is responsible for amylase production in sea bass (*Dicentrarchus labrax*) larvae [67]. Studies showed intestinal microbiota of cultured ayu (*Plecoglossus* *altivelis*), common carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), Japanese eel (*Anguilla japonica*) and tilapia (*Oreochromis niloticus*) produce amylase and 65 isolates out of 206 i.e 31.6% produces more than 0.01 U amylase ml^{-1} and they were characterized as *Aeromonas* spp., *Bacterioidaceae* and *Clostridium* spp. [82]. Grass carp, common carp and tilapia (*Oreochromis mossambica*) were observed for showing higher densities of amylolytic activity but amylolytic strains were not seen in the GI tract of carnivorous fish catfish (*Clarias batrachus*) and murrel (*Channa punctatus*) [30]. An in-vitro study suggested that *Bacillus cereus*, *Bacillus circulans* and *Bacillus pumilus* were isolated from rohu fish and they were good producers of the amylolytic enzyme [48]. Skrodenyte-Arbaciauskiene (2007) isolated 60 different strains of adult roach (*Rutilus rutilus*) fish gut bacteria and a total of 34 showed in vitro amylolytic activity [83]. Though Kar and Ghosh (2008) reported amylase producing bacteria in the gut of Rohu and Murrel they did not identify them and further, Mondal et al. (2008) when documented found that foregut has more amylase producing bacteria in case of *Labeo calbasu* and *Labeo bata* in comparision to hind gut [49, 53]. A large population of amylase producing bacteria were detected in the GI tract of three Indian major carps, catla (*Catla catla*), mrigal (*Cirrhinus mrigala*) and rohu (*Labeo rohita*), the bacteria isolated from the proximal intestine of Catla and Mrigal showed considerably higher amylase production [54]. In a study it was found that the amylase activity of *Pseudomonas* sp. isolated from Atlantic cod is highest with 5.640 U mL^{-1} [84]. In an in-vitro study it was found that in *Cirrhinus mrigala* amylolytic bacteria were found to be highest and they were identified as *Bacillus amyloliquefaciens*[85]. The gut bacteria of omnivorous fishes shows higher activity in producing alpha amylase [86].

This review revealed that amylase-producing bacteria are found in omnivorous fishes more than in carnivorous and herbivorous fishes but the enzyme production varies with diet manipulation. The microorganisms which are a major producer of amylase reside in the foregut rather than the hind gut and these belong to *Bacillus* and *Aeromonas* spp.

6. CHITINASE-PRODUCING GUT BACTERIA IN FISH

Glycosidic bonds in Chitins are hydrolysed by Chitinase. In the intestine of a marine teleost, *Lateolabrax* spp. chitinolytic bacteria were recorded for the first time [87]. The whole GI tract is reported to be showing Chitinolytic activity but the stomach and pyloric tissue show higher activity, indicating that these organs or the diet are the main sources of the enzymes [88]. *Enterobacter, Vibrio* and *Pseudomonas* were considered bacteria with chitinolytic activity while performing experiments with Gray murrel [61]. It was reported that *Aeromonas* spp., and *Vibrio* spp. are chitinase-producing bacteria isolated from the GI tract of tilapia [89]. On the gut microbiota of Dover sole (*Solea solea* L.), it was found that the strains which belong to *Acinetobacter, Enterobacteriaceae, Photobacterium* and *Vibrio*. Study on tilapia (*Sarotherodon niloticus*). It was observed that *Aeromonas caviae, Aeromonas hydrophila, Aeromonas jandaei, Aeromonas sobria* and *Aeromonas veroni* isolated from common carp, crucian carp and gray mullet displayed chitinase activity [90]. The study of Sugita & Ito (2006), reported that 98.8% out of total isolates from the Japanese flounder intestine showed chitinolytic activity and they were identified as *Vibrio fischeri, Vibrio harveyi* and the *Vibrio scophthalmi – Vibrio ichthyoenteri* group [91]. In a study it was found that Pseudomonas spp. isolated from the gut of Atlantic cod can produce different enzymes like- Amylase, Cellulase, Protease, Chitinase etc. 0.085 U Ml^{-1} chitinase is the least producing enzyme [84].

Table 4. Amylase-producing bacteria from GI tract of different fishes

Microorganism	Isolated from	Reference
Strict anaerobes and *Aeromonas hydrophila*	*Ctenopharyngodon idella*	[62]
Vibrio spp.	*Dicentrarchus labrax larve*	[67]
Aeromonas spp, *Bacteroidaceae*, *Clostridium* spp.	*Plecoglossus altivelis, Ictalurus punctatus, Cyprinus carpio, Anguilla japonica, Oreochromis niloticus*	[82]
Bacillus circulans, B. pumilus, B. cereus	*Labeo rohita*	[48]
Aeromonas spp, *Enterobacteriaceae; Pseudomonas* spp, *Flavobacterium* spp	*Rutilus rutilus*	[83]
Bacillus licheniformis, Bacillus subtilis	*Labeo bata*	[50]
Citrobacter spp, *Enterobacter* spp., *Bacillus coagulans, Bacillus cereus.*	*Catla catla, Cirrhinus mrigala. Labeo rohita*	[54]
Bacillus thuringiensis, B. cereus, Bacillus spp,,	*Salmo salar*	[59]

Bacillus subtilis and *Acinetobacter* spp.		

Table 5. Chitinase-producing bacteria from GI tract of different fishes

Microorganism	**Isolated from**	**Reference**
Enterobacter spp., *Vibrio* spp., *Pseudomonas* spp	*Mugil cephalus*	[61]
Aeromonas spp., and *Vibrio* spp.	*Oreochromis niloticus*	[89]
Acinetobacter spp., *Enterobacteriaceae*, *Flavobacterium* spp., *Photobacterium* spp., *Vibrio* spp.	*Solea solea*	[92]
Plesiomonas shigelloides and *Aeromonas hydrophila*	*Oreochromis niloticus*	[93]
Aeromonas caviae, A. hydrophila, A. jandaei, A. sobria and *A. veroni*	*Carassius Carassius, Mugil cephalus, Cyprinus carpio*	[90]
Marinobacter lutaoensis, Ferrimonas balearica, Pseudoalteromonas piscicida, Enterovibrio norvegicus, Grimontia hollisae, Photobacterium damselae spp. damselae, P. leiognathi, P. lipolyticum, P. phosphoreum, P. rosenbergii, Vibrio campbelli, V. chagasii, V. fischeri, V. fortis, V. gallicus, V. harveyi, V. natrigenes, V. nigripulchritudo, V. ordalii, V. parahaemolyticus, V. pomeroyi, V. ponticus, V. proteolyticus, V. rumoiensis, V. shilonii, V. tasmaniensis and V. tubiashii	*Various Japanese costal fishes*	[94]
Vibrio fischeri, V. harveyi, V. scophthalmi, V. iscthyoenteri group type 1, *V. scophthalmi, V. iscthyoenteri* group type 2 and *V. scophthalmi, V. iscthyoenteri* group type 3	*Paralichthys olivaceus*	[91]
Bacillus thuringiensis, Bacillus cereus, Bacillus spp., *Bacillus subtilis* and *Acinetobacter* spp.	*Salmo salar*	[73]

From the Table 5 observation and review, it is evident that Chitinolytic activity is reported to be present throughout the GI tract, and high activity is localized in the stomach and pyloric tissue, indicating that these organs or the diet are the main sources of the enzymes. Most common chitinase-producing microorganisms belong to *Aeromonas, Vibrio*, *Photobacterium* and *Bacillus*.

7. ROLE OF MICROBIOTA IN DIGESTION, IMMUNITY AND DEVELOPMENT OF FISHES

Microbiota largely influence the development of tissue and organ in animals. Enzymes produced by the intestinal microflora in addition to the endogenous sources play a significant role in digestion, especially in the case of plant materials such as cellulose [96]. A study established that the GI microbiota of pinfish (*Lagodon rhomboides*) contribute to the breakdown of plant material [27]. The presence of a high concentration of Aeromonas in the GI tract can play an important role in digestion as Aeromonas species secrete several proteases and chitinase [90, 97]. Wang and Xu (2006) showed a significant difference ($P < 0.05$) in digestive enzyme activity; protease, amylase and lipase in common carp by using *Bacillus* sp. as probiotics [98]. When beneficial bacteria are used with fish feed digestibility, growth and protein efficiency of fish increases because bacteria produce digestive enzymes along with it increase in leukocytes, monocyte, erythrocyte etc. and trigger non-specific immunity [99]. In a later study, four different inclusion levels of *Bacillus subtilis* isolated from *Cirrhinus mrigala* used on survival, feed conversion ratio, specific growth rate, proximate composition, intestinal amylase and protease activity of four live-bearing ornamental fishes. Length, weight, survival, body ash and protein content and gut enzyme activity were significantly improved by including bacilli in the diets, Moreover, improved disease resistance against *Aeromonas hydrophila* infection was noticed in fish-fed bacilli [100]. Sun et al., (2009) reported that bacteria in the fish gut have a significant role in the digestion of food as well as in the immunity of their hosts [101]. Bacteria which can produce enzymes help in the digestion of carbohydrates, proteins, and especially the substrate like cellulose which can be digested only by a few animals. According to Ray et al. (2012), the extracellular enzyme-producing bacteria in fish gut show positive effects on the digestive processes of the host [8].

Mutualistic or pathogenic relationships are the most common type of relationship between fish and surrounding microorganisms. In immune defense, metabolic homeostasis, and nutritional provisioning gut microbiota plays an important role in fishes, humans and other mammals [102, 103]. Moreover, several studies indicated that the fish gut bacteria are linked with disease resistance whereas the fish with disturbed gut microbial composition due to changes in feed or antibiotic treatment increases its susceptibility towards pathogens and developed with declined immunity and nutrition [104–106]. Exogenous enzymes can be produced by the gut microbes which facilitate the digestion of complex and large molecules, such as protein, chitin and starch [107]. In zebrafish, gut bacteria provides direct evidence of epithelial cell proliferation and plays important role in GIT development [108]. Askarian et al., (2011) displayed that beluga (*Huso huso*) and Persian sturgeon (*Acipenser persicus*) when fed with two lactic acid bacteria *(Lactococcus curvatus* and *Leuconostoc mesenteroides*), it enhanced specific growth rate, survival and an increase in the digestive enzyme (amylase, protease and lipase) [109]. It is well studied that probiotics and enzyme-producing bacteria in fish gut influence reproduction in factors like fertilization, gonadosomatic index, fecundity, and production of fry from the females [110]. Similar studies have shown that the bacteria of the gut may involve in the development of gonads as well as the subsequent reproductive success of the host. For example, *Lactobacillus rhamnosus* improves the larval development of zebra fishes as well as improves growth and sex differentiation when administered continuously from birth to sexual maturation [111, 112].

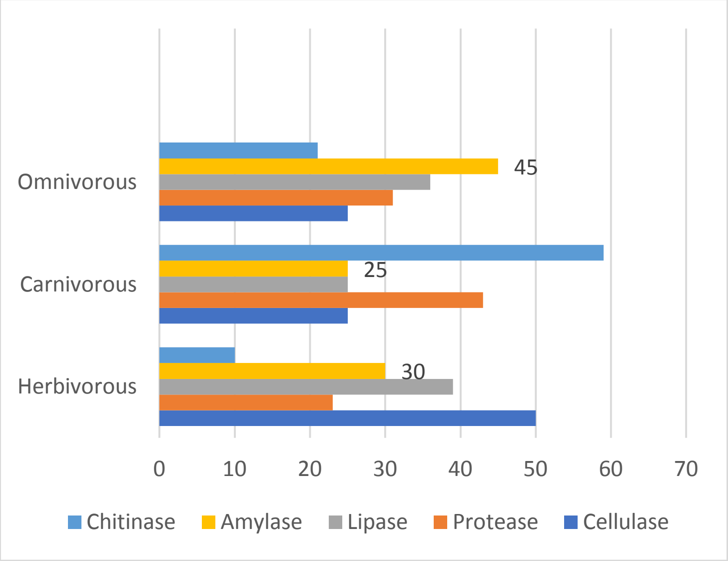

Fig. 1. Bar diagram showing abundance of enzyme producing bacteria according to their feeding habit

Table 6. List of some common bacterial strains found in some fish gut

Fish species	**Bacterial strain**	**References**
Ctenopharyngodon Idella (grass carp)	*Aeromonas* spp.	[55]
Labeo rohita (Rohu)	*Bacillus circulans, Bacillus pumilus Bacillus cereus*	[48]
Heteropneustes fossilis (Asian stinging catfish)	*Bacillus* spp.	[64]
Clarias batrachus (walking catfish)	*Pseudomonas* spp.	[65]
Dicentrarchus labrax (European seabass)	*Vibrio* spp., *Acinetobacter* spp., *Enterobacteriaceae* spp., *Pseudomonas* spp.	[67]
Ictalurus punctatus (channel catfish)	*Aeromonas* spp.	[82]
Oreochromis mossambica (Mozambique tilapia)	*Bacterioidaceae* spp., *Clostridium* spp.	[82]
Cirrhinus mrigala (mrigal carp)	*Bacillus amyloliquefaciens*	[85]
Gadus morhua (Atlantic cod)	*Pseudomonas* spp.	[84]
Channa striata (striped snakehead)	*Enterobecter* spp., *Pseudomonas* spp., *Vibrio* spp.	[61]
Sarotherodon niloticus (Nile tilapia)	*Plesiomonas shigelloides, Aeromonas hydrophila*	[89]
Chanos chanos (Milkfish)	*Pseudomonas* spp., *Vibrio* spp *Enterobacteriaceae*	[95]
Carassius carassius (crucian carp)	*Aeromonas caviae, Aeromonas hydrophila, Aeromonas jandaei, Aeromonas sobria, Aeromonas*	[90]

	veroni.	
Paralichthys olivaceus (olive flounder)	*Vibrio fischeri, Vibrio harveyi, Vibrio scophthalm, Vibrio ichthyoenteri*	[91]

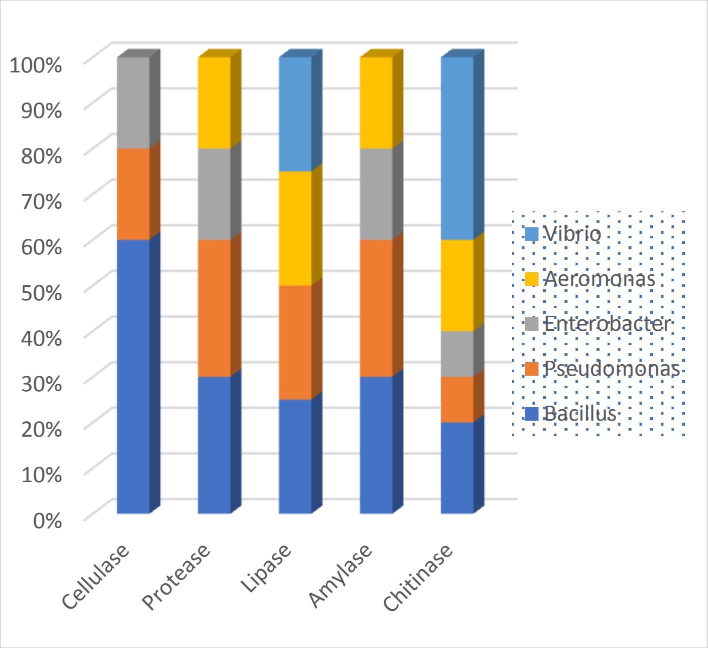

Fig. 2. Diagram showing some common bacterial strain and their contribution in percentage to the type of enzyme they are producing

Table 7. Gut bacteria and their beneficial effect on fish

Name of the bacteria	**Beneficial effect**	**Reference**
Lactobacillus rhamnosus	Enhance immunity and reduce disease susceptibility, improve blood quality.	[122]
Streptococcus spp.	Improve feeding efficiency and growth rate.	[123]
Bacillus amyloliquefaciens	Enhance antibody concentration, and reduce stress.	[124]
Lactobacillus spp.	Reduce pathogen load.	[106]
Bacillus cereus	Protect from Aeromonas hydrophilia infection.	[125]
Bacillus spp.	Reduce the load of ammonia and nitrate.	[126]
Nitrosomonas spp.	Reduce pathogen load.	[127]
Enterococcus faecium	Enhance immunity.	[128]
Bacillus subtilis	Enhance cellular immunity.	[129]
Alcaligenes spp.	Enhance volatile short-chain fatty acids.	[130]

It has been proven through experiment that in grass carp (*Ctenopharyngodon idella*) the change in the composition of gut bacteria, biosynthesis, and metabolic pathways of carbohydrates, amino acids and lipids also change [113]. Further, In a study on zebrafish, it was observed that the epithelial absorption of fatty was promoted by the colonization of gut bacteria [114]. When a fish is growing from egg to larvae to adult the bacterial composition also changes and increases [115].

Bacteriocin nisin Z was produced from *Lactococcus lactis* isolated from some marine fishes, which can prevent the development of the fish microbe *Lactococcus garvieae* at 5 AU mL-1. Because of this, it becomes a promising option for the prevention of *lactococcosis* [116]. A bacterium *Centroscyllium fabricii* isolated from the deep sea shark was found to have an antagonistic activity in the fish gut [117].

Nile tilapia (*Oreochromis niloticus*) fed with a probiotic strain of *Lactobacillus* sp. shows enhancement of crude lipid, total protein, and body weight [118]. Growth and survival rate increase in *Xiphophorus helleri*, *Xiphophorus maculates*, and *Poecilia reticulate* fed with probiotic supplemented food containing *Bacillus subtilis* and *Streptomyces* sp.

[119]. According to He et al. (2017) *Bacillus* and *Lactobacillus*, two common probiotic genera of bacteria used in aquaculture, can stimulate the expression of inflammatory cytokines in the fish gut [106]. In Javanese carp (*Puntius gonionotus*), significant weight gain can be seen in fishes fed with *Enterococcus faecalis* compared to the control group of carp [120]. The enzyme-producing bacteria from the gut of experimental fish may play an important role in the digestion process of the fish [121].

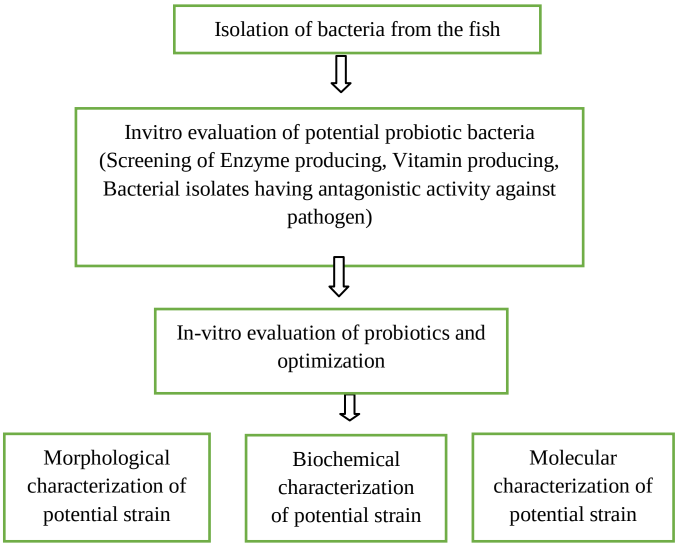

Fig. 3. Schematic representation of screening process for potential probiotic gut bacteria

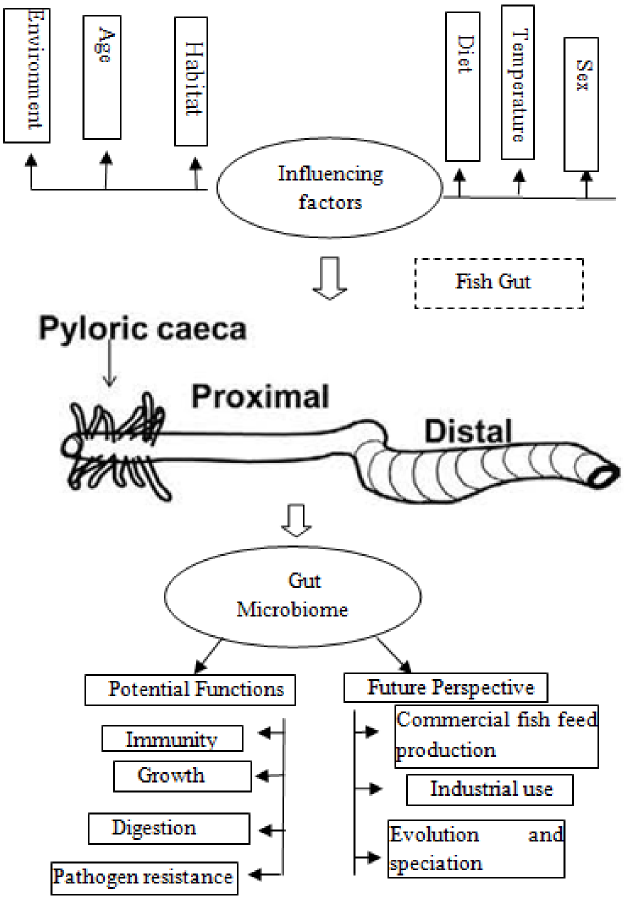

Fig. 4. Showing factor influencing gut bacteria of fishes along with potential function and future perspective

Table 8. Some species-specific bacterial strains and their benefits on fish health

Name of the fish	Dominant Strain	Benefit	Reference
Japanese eel (*Anguilla japonica*), carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), channel catfish (*Ictalurus punctatus*) Ayu (*Plecoglossus altivelis*) and tilapia (*Tilapia nilotica*)	Bacteroides type A	producing vitamin B12	[131]
Ayu (*Plecoglossus altivelis*), carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), Japanese eel (*Anguilla japonica*) and Tilapia (*Tilapia nilotica)*	*Aeromonas, Bacteroidaceae* and *Clostridium*	Producing amylase that plays an important role in the digestion of starch	[82]
Rohu (*Labeo rohita*) and catla (*Catla catla*)	*Enterococcus faecalis* and *Pediococcus acidilactici*	Ferment fish processing waste	[132]
Rohu (*Labeo rohita*), Mrigal (*Cyrrhinus mirgala*) and Tilapia (*Oreochromis mossambicus*)	*Enterobacter asbura, Pichia kudriavzevii, Candida tropicalis* and *Candida parapsilosis*	Produce tannase to overcome the antinutritional factors in the feedstuffs.	[133]

8. CONCLUSION

From this review, it is evident that various gut bacteria of fishes helps in growth, digestion, immunity, disease resistance etc. Therefore, it can be recommended to use these beneficial bacteria as probiotics. When it comes to the hypotheses of whether the gut microbiota can contribute to nutrition or not, it can be concluded that gut microbiota may contribute to nutrition to some extent in-vivo but further investigations are required related to the fact that in-vitro and industrial use of these can be beneficial or not. Although a huge number of bacteria are associated with the gut of fish beneficial bacteria are more important. It is revealed from the review that Carp fishes have most studies on enzyme-producing gut bacteria therefore, the contribution of other fish specie's gut bacteria is need to be studied. The major benefit of cellulase producing bacteria is that it helps in digestion of plant material as most of the animal cannot produce its own cellulase. But further cellulase producing bacteria such as *Bacillus* spp. can also be beneficial for fish in growth, immunity etc. Similarly, various *Aeromonas* spp. produce chitinase, amylase and protease as well. From the review it has been noted that the benefits of enzyme producing bacteria are described vaguely. Therefore, some specific information and research are necessary on each enzyme producing bacteria and their significance on fish health. As these clear understanding may lead to proper use of these bacteria in production of commercial fish feed. The study on chitinase producing fish gut bacteria needs more focused study as it might be useful as a constitutive material in formulated fish feed. The influence of chitin on disease resistance, susceptibility and innate immune parameters etc. are still not fully understood and require further investigation. Over the last 20 years, various comprehensive review papers have been published targeting the use of probiotics related to immunity, growth, and prevention of diseases and bacteria. From our point of view, we recommend the use of mixture of beneficial bacteria (consortium) to evaluate growth, feed conversion rate, gut enzyme activity, gut maturation, gut immunity, modulation of the gut microbiota and disease resistance. For formulation of such beneficial probiotic consortia this review will play a significant role in providing data.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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