Review Article

Exploring the impact of probiotics on the gut ecosystem and morpho-histology in fish: current knowledge

Abstract

As global demand for fish as a food source continues to rise, addressing challenges within the aquaculture industry and meeting consumer needs becomes imperative. Enhancing fish growth and safeguarding against microbial pathogens are among these challenges. Understanding the intestinal microbiome holds promise for achieving these goals and benefiting the aquaculture sector. Probiotics, live microorganisms administered at appropriate levels, can foster a balanced gut microbiota in animals. This can yield advantages like pathogen defense, improved digestion, enhanced growth, and increased survival rates. Probiotics are emerging as tools to promote healthy intestinal environments in fish species, with potential to positively influence gut structure, ecosystem, growth, and disease resistance. The dynamic interplay between fish and their intestinal microbiota has garnered significant attention, affecting fish health, performance, and overall well-being. This review compiles research findings on the influence of probiotics on fish intestinal ecosystems, morpho-histological structures, and enzymatic activities. It outlines their impact on gut microbiota composition, demonstrating their ability to increase beneficial bacteria while reducing pathogenic strains. Probiotics can enhance intestinal morphology, promoting villi development, goblet cell density, and mucous layer thickness. Additionally, they influence digestive enzyme activity, resulting in improved nutrient absorption and fish growth. Although this field is continually evolving, the progress in deciphering probiotics' complex interactions with fish guts underscores their potential benefits.

Key words: Probiotics, fish and shellfish, gut microbiota, intestine, histology, morphology, digestive activity, enzymatic activity

Introduction

With the increasing demand for fish as food, it is important to address the challenges of the industry and meet the needs of consumers. One of the challenges is the need to improve fish growth and protect them from microbial pathogens (Ghori et al., 2018; Lertwanakarn et al., 2021; Syanya, Litabas, et al., 2023). By understanding the intestinal microbiome, valuable insights can be gained to achieve these goals and provide useful information to the aquaculture industry(Dhillon & Bhatnagar, 2020; Diwan et al., 2022; Yukgehnaish et al., 2020). Probiotics are living microorganisms that, when administered at appropriate doses, can promote a healthy balance of gut bacteria in animals. This can result in various benefits such as preventing the invasion of harmful pathogens, improving digestion, promoting growth, and increasing survival rates (Galagarza et al., 2018; Haraz et al., 2023; Waiyamitra et al., 2020).In this context, probiotics have emerged as promising tools to promote and maintain a healthy intestinal environment in fish species(Abdel-Latif et al., 2023; Midhun Sebastian Jose et al., 2023; Syanya, Mathia, et al., 2023). By providing beneficial microorganisms, probiotics have the potential to positively influence the intestinal structure and ecosystem of fish, resulting in improved growth, disease resistance, and overall performance (Bondad-Reantaso et al., 2023; Kuebutornye et al., 2019; Melo-Bolívar et al., 2021; Vallejo-Cordoba et al., 2020). To understand the impact of probiotics, it is essential to delve into the concept of the fish gut ecosystem(Thanh et al., 2021a; Xia, Yu, et al., 2020a).The complex relationship between fish and their intestinal microbiota has become a fascinating area of research in recent years(Amoah et al., 2023; Foysal et al., 2019). Among the various factors influencing the well-being of fish, the composition and functionality of their intestinal microbiota have received particular attention (Foucault et al., 2022; Z. Li et al., 2023; Luan et al., 2023; Toxqui-Rodríguez et al., 2023).Understanding the effects of probiotics on the intestinal structure and ecosystem of fish is essential for advancing aquaculture practices, sustainable fish production, and overall ecosystem health(Gallo et al., 2020). While the field is still evolving, significant progress has been made in unraveling the complex interactions between probiotics and the fish gut (Foysal et al., 2019; Lalitha et al., 2022; Thanh et al., 2021b). This review aims to compile information from research findings on the influence of probiotics on the ecosystem and morpho-histology of the host fish's intestine. It will provide a comprehensive overview of this topic and predict future perspectives on the use of probiotics in aquaculture.

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Methods

Various studies evaluated by peers and published in different journals on the impact of probiotic use in aquaculture on the structure and environment of fish intestines have been assessed and understood using a systematic research design in this article review. For a more concise update, the consulted articles are those published in approximately five and a half years, ranging from 2018 to 2023 (except for publications that provide general informations on certain topics). This review is limited to the results of original research conducted on the use of probiotics in finfish worldwide, and these results should include the effects on the structure and environment of the intestines. Platforms such as Google Scholar, ProQuest, indexing databases like Scopus, Web of Science, PubMed, publishers like Elsevier (ScienceDirect), Springer Nature, Wiley, Taylor and Francis, and journal websites were consulted to gather a total of 135 published articles used as literature sources for this review. Thanks to its irreplaceable effectiveness in tracking the evolution of a scientific principle, the review conducted here is of the narrative type.

Impact of probiotics on gut microbiota

The fish gut microbiota plays a crucial role in digestion, nutrient absorption, immune system regulation, and overall health(Diwan et al., 2023; Ibrahem, 2013; Luan et al., 2023; Monzón-Atienza et al., 2023; Ringø et al., 2016). The impact of probiotics on fish gut microbiota can be both positive and complex, and it largely depends on various factors such as the species of fish, the specific probiotic strains used, the dosage, and the environmental conditions (El-Saadony et al., 2021; Fijan, 2014; Talwar et al., 2018; H. J. Wu & Wu, 2012; Wuertz et al., 2021; Zhao et al., 2023).The administration of probiotics has been demonstrated to positively influence the composition and diversity of the intestinal microbiota in fish(Ghori et al., 2022; Hasan et al., 2023). Several studies have been conducted to assess the effects of probiotics on the composition of the gut microbiota in different species of fish and its interactions with beneficial and pathogenic bacteria(Egerton et al., 2018; Ringø et al., 2022).The research on tilapia, which appears to have received increased attention from researchers on this topic in recent years, is shown in Table 1.

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The administration of *Lactococcus lactis* JCM5805 disrupts the abundance of intestinal bacteria and alters the profiles of intestinal microbial metabolites. This supports the hypothesis that this strain affects the composition of the intestinal flora community, modifies intestinal metabolism, and ultimately improves the host's growth and immunity(Xia, Wang, et al., 2020a). Additionally,multi-species probiotic supplementation in Pangasianodonhypophthalmus fry increased the diversity and richness of the gut microbiota, contributing to improved gut health and disease resistance(Abdel-Latif et al., 2023).Probiotics play a role in shaping the total number of bacteria in the fish intestinal tract. For instance, in a study by Hassaan et al. (2018), the application of B. subtilis as a dietary supplement with malic acid resulted in a significant decrease in the total number of bacteria in the intestines and feces of Nile tilapia. Similarly, Deng et al. (2022a) demonstrated that different farming systems influenced the composition of the intestinal microbiota, with *B. subtilis* supplementation leading to increased abundance of beneficial bacteria in fish intestines. In another study by Galagarza et al. (2018), the administration of ~~*Bacillus*~~*B. subtilis* endospores in Nile tilapia feed resulted in increased microbial diversity and stability in the gut ecosystem.Moreover, Haraz et al. (2023) showed that using the biofloc system with probiotics led to the highest total number of bacteria in the intestinal microbiota of Nile tilapia, as compared to the conventional system.In the same context, probiotics play a dual role, reducing the number of certain groups or phyla while simultaneously promoting the increase of other groups. Various studies have demonstrated the positive impact of probiotic supplementation on the growth of beneficial bacteria, such as lactic acid bacteria, *Bacillus spp*., and other potential probiotic strains, while concurrently inhibiting the proliferation of harmful bacteria (EtyemezBüyükdeveci et al., 2023a; Giri et al., 2018, 2019; Pillinger et al., 2022).For instance, Poolsawat et al. (2020) employed high-throughput sequencing and found higher levels of the three main phyla - planctomycetes, proteobacteria, and chloroflexes - in all groups supplemented with probiotics *Clostridium butyricum* compared to the control group. Additionally, Xia et al. (2018) conducted a study on Nile tilapia's intestinal microbiota, revealing a significant decrease in the genus Plesiomonas (potential pathogens) and a notable increase in potentially probiotic *Rhizobium* and *Achromobacter* in groups fed with probiotics *Lactobacillus rhamnosus* JCM1136 and *Lactococcus lactis* subsp. *lactis* JCM5805.Moreover, the introduction of *Bacillus subtilis* var. *natto* as a feed supplement also influenced the gut microbial composition in Nile tilapia. This supplementation significantly increased *Lactobacillaceae*, *Firmicutes*, *Chromatiales*, and *Rhodobacteria*, as well as the *Firmicutes*/*Bacteroidetes* ratio (Pan et al., 2023). Similarly, the administration of *Rummeliibacillusstabekisii* as a probiotic in Nile tilapia resulted in a substantial increase in the abundance of potentially probiotic bacteria from the genera *Bacillus* and *Lactobacillus* spp., while reducing the abundance of potential pathogenic bacteria, such as *Streptococcus* and *Staphylococcus* spp. (Tan et al., 2019).Additionally, Zhang et al. (2019) concluded that feeding tilapia a diet containing *Bacillus velezensis* LF01 could potentially impact the intestinal flora by promoting the accumulation of more beneficial microorganisms and inhibiting the growth of potential pathogens, such as Edwardsiella and Plesiomonas. This positive effect of probiotics on the intestinal microbiota was further supported by the study conducted by Tachibana et al. (2020, 2021). They observed that *~~Bacillus~~ B.subtilis* and *Bacillus licheniformis* supplementation led to higher richness and habitability indices in the Nile tilapia's intestines, along with changes in bacterial phyla composition, including a decrease in the percentage of *Proteobacteria* and an increase in potentially probiotic phyla Firmicutes, Fusobacteria, and Bacteroidetes.

Probiotics are capable of favorably modulating the fish's intestinal microbiota by promoting the growth of beneficial bacteria and inhibiting the proliferation of pathogenic bacteria. This can lead to an improvement in the diversity of the intestinal microbiota and the overall health of the host. The interactions between probiotics and the intestinal microbiota play a crucial role in these beneficial effects. As a result of these phenomena, there is a significant improvement in the survival and growth of fish fed with probiotic supplementation. Similarly, probiotics create and maintain a favorable environment in the intestinal tract, as evidenced by Liu et al. (2021) who demonstrated that the high survival rate of tilapia against S. agalactiae could be attributed to the fact that *B. subtilis* and *E. faecalis* provided a better micro-ecological intestinal environment. Maas et al. (2021) analyzed microbial networks and also showed that supplementing with strains of *Bacillus amyloliquefaciens* as probiotics with enzymes improved microbial interactions while increasing the abundance of lactic acid bacteria and Bacillus species.

Probiotics significantly impact the microbial composition of fish gut microbiota by introducing beneficial microorganisms or enhancing existing growth. This shift in microbial populations leads to a more diverse and healthier gut microbiota, improving digestion, nutrient absorption, and overall fish health. Probiotics engage in competitive exclusion, limiting harmful microbes' growth and creating space for beneficial ones. They also produce metabolites like short-chain fatty acids, which promote beneficial bacteria growth while inhibiting pathogen proliferation. The introduction of probiotics can result in increased beneficial bacteria, which improve digestion and disease prevention. Additionally, the competition-driven decrease in harmful microbes is crucial for preventing infections and diseases. The microbial composition altered by probiotics can lead to a shift towards greater diversity, which is associated with improved gut function and resilience.

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Table 1

Effects of some probiotics in the gut of Tilapia

Probiotic species	Host species	Effects in host gut (in comparison to the control group.)	Reference
Bacillus subtilis (+ malic acid)	Nile tilapia	Reduction of intestinal pH; decrease in the intestinal bacterial count	(Hassaan et al., 2018)
Bacillus species (TCMBS) + herbal	Nile tilapia	Significant increase in β-defensin and lysozyme	(Abarike et al., 2018)
Bacillus subtilis (endospores)	Nile tilapia	Positive regulation of gene expression of the two pro-inflammatory cytokines TNF-α and IL-1β	(Galagarza et al., 2018)
Lactobacillus rhamnosus JCM1136 &Lactococcus lactis subsp. lactis JCM5805	Nile tilapia	Higher expression of immunity-related genes TNF-α, IFN-γ, lysozyme (lyzc), heat shock protein 70 (hsp70), and IL-1β; Significant increase in intestinal microvillar density and length; Significant reduction of Plesiomonas (potential pathogens); Significant increase in Rhizobium and Achromobacter (potential probiotics).	(Xia et al., 2018)
Rummeliibacillusstabekisii	Nile tilapia	Increase in the abundance of potential probiotics (Bacillus and Lactobacillus spp.); Reduction in the abundance of potential pathogenic bacteria (Streptococcus and Staphylococcus spp.); Significant increase in intestinal digestive enzymes protease, cellulase, and xylanase	(Tan et al., 2019)
Bacillus velezensis LF01	Nile tilapia	Significant increase in genes related to the immune system (C3, lysozyme c, and MHC-IIβ); Accumulation of more beneficial microorganisms; Inhibition of the growth of potentially pathogenic Edwardsiella and Plesiomonas	(D. Zhang et al., 2019)
Lactococcus lactis JCM5805	Nile tilapia	Alteration of intestinal bacterial abundance; Modification of intestinal microbial metabolic profiles; Strong correlation between certain families of intestinal flora and altered metabolites	(Xia et al., 2020b)
Bacillus cereus NY5, bacillus subtilis	Nile tilapia	Significant increase in length and density of intestinal microvilli; significant increase in expression of the lysozyme type c gene (lyzc); Substantial enhancement of indigenous intestinal bacterial communities in tilapia (potential probiotics).	(Xia et al., 2020a)

Table 1*(continued)*

Probiotic species	Host species	Effects in host gut (in comparison to the control group.)	Reference
Clostridium butyricum	Red Tilapia (O. niloticus x O. aureus)	Significant increase in villus height; Reduction of intestinal E. coli count; Increase in potentially probiotic phyla (Planctomycetes, Proteobacteria, Chloroflexes).	(Poolsawat et al., 2020)
Bacillus amyloliquefaciens	Nile tilapia	Increase in proximal fat content; Improvement in digestibility of crude proteins, calcium, and phosphorus; Enhancement of microbial interactions; Increase in the abundance of lactic acid bacteria and Bacillus species.	(Maas et al., 2021)
Bacillus subtilis & Enterococcus faecalis	Nile tilapia	Increase in lipase activity, sucrase-isomaltase (SI) activity, lysozyme (LYZ) activity, complement component C3 activity, total antioxidant capacity (T-AOC), and catalase (CAT) activity; Improvement in length, width, and muscular thickness of intestinal villi; Enhancement of the intestinal microecological environment.	(Liu et al., 2021)
Clostridium autoethanogenum (its protein)	Gift Nile tilapia	Increase in sodium/potassium-ATPase transporter; Decrease in malondialdehyde (MDA) content; Increase in glutathione (GSH) content and superoxide dismutase (SOD) activity; Regulation of kelch-like ECH-associated protein 1 (Keap1), nuclear factor erythroid 2-related factor 2 (Nrf2), and glutathione peroxidase (GPx); Regulation of target of rapamycin (TOR) immune target, peptide transporter 1β (Pept 1β), complement component 3 (C3), and interferon gamma (IFN-γ); Regulation of transforming growth factor beta (TGF-β) by 5% and 10% CaP.	(Maulu et al., 2021)
Bacillus subtilis & Bacillus licheniformis	Nile tilapia	Increase in the abundance of Fusobacteria and Bacteroidetes phyla, and a lower percentage of Proteobacteria; Improvement in enzymatic activities in the anterior, medial, and posterior portions of the intestine.	(Tachibana et al., 2021)
Bacillus subtilis spores	Nile tilapia	Increase in the relative abundance of Cetobacterium, Gemmobacter, and Bacillus.	(Deng et al., 2022b)
Vibrio sp. & Bacillus cereus	Nile tilapia	Significant increase in intestinal activity of α-amylase, cellulase, and protease	(Hortillosa et al., 2022)

Table 1*(continued)*

Probiotic species	Host species	Effects in host gut (in comparison to the control group.)	Reference
Lactobacillus reuteri	Nile tilapia	Significant increase in villus height and mucin secretion; Improvement in trypsin, lipase, and amylase activities in different intestinal segments; Increase in expression levels of hif1α, zo-1, and occludin in the anterior, middle, and posterior intestine; Enhancement of α-diversity indices (Shannon and Simpson) of the intestinal microbiota; Increase in Proteobacteria and Actinobacteria; Reduction of Fusobacteria; Increase in bacterial species diversity and interrelations.	(W. Li et al., 2022)
Bacillus subtilis & Lactobacillus acidophilus	Nile tilapia	Highest total number of intestinal microbiota bacteria; Positive impact on digestive enzyme activity (lipase and amylase); Improvement of intestinal morphology of Nile tilapia	(Haraz et al., 2023)
Bacillus subtilis var. natto	Nile tilapia	Significant increase in Lactobacillaceae, Firmicutes, Chromatiales, and Rhodobacteria; Significant increase in altered major bioactive metabolites, peonidine-3-glucoside, L-Tyrosine, 1-Deoxy-1-(N6-lysino)-D-fructose; Increase in palmitoleic acid, 5-KETE, and tangeretin; Improvement in the intestinal immune network	(Pan et al., 2023)
B. subtilis, B. licheniformis & B. pumilus	Nile tilapia	Increase in whole intestinal lengths, heights of anterior and terminal intestinal villi, and the number of anterior goblet cells	(Elsabagh et al., 2018)
Bacillus mojavensis B191 & Bacillus subtilis MRS11	Nile tilapia	Increase in goblet cells, intestinal villus length, microvillus length, microvillus density, and perimeter ratio in the intestine	(EtyemezBüyükdeveci et al., 2023a)
B. amyloliquefaciens, B. subtilis, B. licheniformis, B. pumilus	Nile tilapia	Alteration in the length of intestinal villi across the three intestinal segments; changes in inter-villus space measurements in the anterior portion of the intestine; increased number of goblet cells in the anterior intestine.	(Ghalwash et al., 2022)

Influence of probiotics on intestinal morpho-histology

Probiotics can have notable effects on the structure of the intestines, affecting aspects like villi height, crypt depth, and surface area. Increased villi height leads to better digestion and nutrient absorption, improving overall fish growth and health(Ahmad et al., 2022; ~~P.~~ Chen et al., 2022; Obianwuna et al., 2023). Probiotics can influence histology by affecting cellular morphology, organization, and differentiation within the intestinal lining. They promote healthy cellular arrangement within the intestinal epithelium, maintaining tight junctions between epithelial cells, which play a crucial role in preventing leaky gut syndrome(Ahmed et al., 2022; Jha et al., 2020; Yadav & Jha, 2019). Goblet cells, specialized cells in the intestinal lining, produce mucus, which can be stimulated by probiotics to reinforce the mucosal barrier, shielding the gut from pathogens and maintaining proper gut function (Duangnumsawang et al., 2021; Gyawali et al., 2023; Martini et al., 2017; Pelaseyed et al., 2014; S. Yang & Yu, 2021; Zheng et al., 2020).

Usuallybacterial strains(Borges et al., 2020; Langlois et al., 2021; ~~H. dong~~Li et al., 2019; ~~A. R~~. Wang et al., 2018) or yeast (Islam et al., 2021; Jahan et al., 2021; Reyes-Becerril et al., 2021; Siddik et al., 2021; Zhaxi et al., 2020) probiotics can influence the intestinal environment and have effects on the morphology and histology of fish intestines. They can also play a reparative role in the damaged intestines of fish(Shang et al., 2021; ~~H. L.~~Yang et al., 2022).Probiotics have been shown to positively influence fish intestinal morphology, mucosal thickness, goblet cell density, and epithelial cells proliferation.

Numerous studies have demonstrated that probiotics positively influence the structure and intestinal morphology of fish (Hossain et al., 2022; Jahan et al., 2021; Tabassum et al., 2021). They can improve the development of the intestinal mucosa (Ngamkala et al., 2020; Nimalan et al., 2022, 2023), leading to an increase in the height and surface area of the villi(Kuebutornye et al., 2020; ~~D. X.~~Zhang et al., 2019). Villi are small finger-like projections in the intestinal wall that play a crucial role in nutrient absorption for fish (Lin et al., 2020)as well as for shrimp (Amoah et al., 2019; Liang et al., 2020; ~~J. J.~~Zhang et al., 2020). Intestinal villi serve a dual purpose: they not only absorb nutrients from the animals but also possess the ability to discourage the colonization of harmful bacteria (~~G.~~ Yang et al., 2019, 2021). Healthier and more developed intestinal morphology can enhance nutrient absorption efficiency and improve the overall digestive capacity of fish (Jiang et al., 2022; Laice et al., 2021; ~~W.~~ Li et al., 2021). For example, Chouayekh et al. (2023)demonstrated that the probiotic *Bacillus amyloliquefaciens* US573 increased the length and abundance of villi in

European sea bass. Similarly, in synergy with β-glucan, *Lactobacillus plantarum* significantly increased the length of tilapia intestine villi (Dawood et al., 2020). Interestingly, Lactobacillus plantarum had no effect on the length and thickness of rainbow trout (Oncorhynchus mykiss) villi after 90 days of feeding (Enferadi et al., 2018), but significantly increased the villi height in the same species after 60 days of trials (Dabbagh et al., 2021) and the villi length in tilapia after 14 days of dietary supplementation (Dawood et al., 2019). *Lactobacillus helveticus* also positively improved the height and width of the villi in pond loach (*Misgurnusanguillicaudatus*) after 8 weeks of dietary supplementation(~~G.~~ Yang et al., 2021). Similarly, in a 56-day experiment, the strains *Bacillus coagulans*, *B. licheniformis*, and *Paenibacilluspolymyxa* significantly increased the height and width of intestinal villi in northern whiting (*Sillagosihama*) (Amoah et al., 2019).*Bacillus mojavensis* B191 and *Bacillus subtilis* MRS11 also can affect the structure of intestinal villi in Nile tilapia. In fact, (EtyemezBüyükdeveci et al., 2023b)found that the height and density of microvilli were significantly higher in fish fed with a diet supplemented with *Bacillus mojavensis* B191 and/or *Bacillus subtilis* MRS11. Additionally, the fish treated with probiotics appeared to have a healthy brush border with organized and tight microvilli structures compared to those fed a probiotic-free diet.

Probiotics also stimulate the proliferation of epithelial cells lining the intestine (Suryaningsih et al., 2021), which can help maintain the integrity and barrier function of the intestine (González-Félix et al., 2018). It has also been demonstrated that probiotics increase the thickness of the mucous layer in the fish intestine (A. Nikiforov-Nikishin et al., 2022; D. Nikiforov-Nikishin et al., 2022)and shrimps (Li et al., 2019; Liang et al., 2020). A thicker mucous layer can offer better protection against pathogens and toxins (Amoah et al., 2023). Multi-species probiotics promote an increase in the muscular thickness of the intestine in Nile tilapia (Hossain et al., 2022; Islam et al., 2021). Similarly, an increase in the muscular thickness of the intestine in herbivorous carp (*Ctenopharyngodonidella*) has been observed (Chen et al., 2020). Kong et al. (2021) also made similar observations when supplementing the diet of Northern snakehead (*Channa argus*) with the lactic acid bacteria *Lactococcus lactis* L19 and *Enterococcus faecalis* W24.

Probiotics also affect the intestinal histology of fish by influencing goblet cells (Jayaprakash & Parvathi, 2019; Melo-Bolívar et al., 2023; MirabdollahElahi et al., 2020; Oliveira et al., 2022). Studies have reported that probiotics can lead to changes in the number and size of goblet cells in the intestinal epithelium (Jaramillo-Torres et al., 2019; ~~G~~. Yang et al., 2019), especially by increasing their density (Al-Hisnawi et al., 2019; Haque et al., 2021), resulting in increased mucus production, which contributes to the health and integrity of the intestine (Al-Yassir et al., 2021). Indeed, goblet cells are responsible for mucus production (Back et al., 2020), which serves as a protective barrier for the intestinal wall (Qin et al., 2020; ~~Y.~~ Wu et al., 2022). An increase in the number of goblet cells can enhance the mucosal defense of the intestine, thus reducing the risk of pathogen invasion (Spirina et al., 2019) and inflammation (Du et al., 2021). In their study, (EtyemezBüyükdeveci et al., 2023b) showed that tilapia fed with a diet containing the probiotics *Bacillus mojavensis* B191 and *Bacillus subtilis* MRS11 had a greater number of goblet cells along the epithelium compared to those fed with a regular diet. The results of Gaffar et al. (2023) study also indicated that the use of commercial multi-species probiotics significantly improved mucus-secreting goblet cells and mucous fold enlargement in Gangetic mystus (*Mystuscavasius*). Similarly, *Bacillus amyloliquefaciens* US573 promotes an increase in the number of goblet cells in European seabass(Chouayekh et al., 2023).

Impact of probiotics on enzymatic and digestive activities

The digestive and enzymatic systems of fish are indispensable for facilitating the absorption of nutrients derived from their food sources. The intricate compounds present in fish diet must undergo decomposition into smaller, more readily absorbable constituents, enabling their utilization for energy, growth, and various physiological functions(Assan et al., 2022; Maulu et al., 2021).Enzymes represent biological molecules that facilitate chemical reactions within living organisms. In the context of fish, multiple categories of macromolecules, including proteins, carbohydrates, and lipids, undergo enzymatic hydrolysis into smaller subunits. This process is essential to enable subsequent absorption across intestinal walls. Numerous pivotal enzymes, such as proteases, amylases, and lipases, are involved in the degradation of these macromolecules(Assan et al., 2022). The utilization of probiotics in fish aquaculture holds promise in influencing enzymatic and digestive activities. The interaction between probiotics and the digestive system is multifaceted, involving the enhancement of enzyme activity and the subsequent improvement of nutrient absorption. This has implications for the growth, health, and overall performance of fish in aquaculture systems.Supplementation with probiotics and enzymes enhances nutrient availability, intestinal health, and microbiome stability by augmenting enzymatic digestion of nutrients like calcium, phosphorus, and crude proteins within the proximal and mid intestines(Maas et al., 2021; Tachibana et al., 2021).Research indicates that specific strains of probiotics possess the capability to enhance the activity of digestive enzymes such as proteases (Hassaan et al., 2018), amylases, lysozymes, and lipases (Fei et al., 2018) within the intestines of fish. Consequently, the production of extracellular enzymes has been a pivotal consideration in the selection of probiotics to improve food digestibility, nutrient availability, and host growth (Dawood et al., 2019; Hortillosa et al., 2022).

Used as a probiotic, *Rummeliibacillusstabekisii* has the potential to significantly enhance the production of intestinal digestive enzymes such as protease, cellulase, and xylanase, as demonstrated in the study by Tan et al. (2019) involving Nile tilapia. Similarly, strains Bacillus cereus CC27 and Vibrio sp. CC8, isolated from milkfish, can positively enhance intestinal protease activity, intestinal cellulase activity, and amylase activity in Nile tilapia (Hortillosa et al., 2022). The addition of probiotics to a biofloc system can exert a positive impact on digestive enzyme activities, particularly the fish's lipase and amylase. In this context, the introduction of Lactobacillus acidophilus and Bacillus subtilis probiotics into the biofloc system has shown to positively influence lipase and amylase enzyme activities in Nile tilapia (Haraz et al., 2023). The expression of the lysozyme gene can be significantly augmented through the incorporation of probiotics into the fish's habitat and diet. These beneficial bacteria can thereby stimulate the fish's immune system, consequently elevating lysozyme enzyme synthesis.A study conducted by Xia et al. (2020)substantiates this observation by demonstrating that the supplementation of probiotics Bacillus subtilis and B. cereus NY5 significantly elevated the expression of the lysozyme c-type gene in juvenile tilapia.Certain strains of probiotics can influence lipase activity and fat digestion by exhibiting a positive correlation between specific probiotic bacterial strains and heightened lipase enzyme activity in the digestive system. For instance, strains like Enterococcus faecalis and Bacillus subtilis demonstrate their association with lipase, LYZ, CAT, C3, T-AOC, and SI activities in tilapia (Liu et al., 2021).Probiotic-enriched feeds can enhance the functionality of digestive enzymes within fish intestines, concurrently raising levels of antioxidant enzymes to fortify resistance against oxidative stress. This augmentation can lead to improved cellular health and heightened oxidative stress resistance. An illustrative instance involves the combination of *Bacillus licheniformis* HGA8B and *Paenibacilluspolymyxa* HGA4C, which, when administered to Nile tilapia, significantly elevated both antioxidant and digestive enzymes in the intestine (~~Midhun Sebastian~~ Jose et al., 2023). A diverse range of fish enzymes can be enhanced through the introduction of a monospecific probiotic. This suggests that the probiotic's effects may extend to various aspects of fish biology beyond specific

Formatted: Font color: Red, Strikethrough enzyme types. For instance, activities of protease, amylase, catalase, superoxide dismutase, and lysozyme were notably enhanced through supplementation with Bacillus velezensis GY65 in supplemented groups compared to control groups in mandarin fish (~~J.~~ Wang et al., 2021).Various segments of the intestine may exhibit pH variations, nutrient availability, and other factors that influence the types of microorganisms present. Probiotics could potentially exert targeted effects on these local conditions, resulting in variations in enzymatic activities. The application of probiotics can also lead to distinct enzymatic activities in different parts of the intestine. This implies that probiotics might have influenced local microbial communities and the production of specific enzymes in each intestinal section. For instance, the middle, anterior, and posterior portions of the intestine showed distinct enzymatic activities after the application of Bacillus licheniformis and *Bacillus subtilis* in Nile tilapia(Tachibana et al., 2021). Furthermore, dietary supplementation of Nile tilapia with Lactobacillus plantarum and Bacillus subtilis stimulated specific amylase activity in the anterior intestine (Guimarães et al., 2021).

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By enhancing the activity of these enzymes, probiotics contribute to a more efficient process of digestion. This, in turn, can lead to improved nutrient absorption, thereby promoting fish growth and overall health. Indeed, the heightened enzymatic activity resulting from probiotic supplementation facilitates the breakdown of dietary components, such as proteins, carbohydrates, and lipids. This decomposition into smaller, easily digestible units allows the fish to more effectively absorb essential nutrients. As a result, fish receiving probiotics as part of their diet are likely to exhibit enhanced food utilization and improved growth rates. The synergy among probiotics, digestive enzymes, and nutrient absorption underscores the potential of probiotic interventions not only to enhance fish health but also to contribute to the efficiency and sustainability of aquaculture practices.

Conclusion

When fish possess a healthy intestinal environment and enhanced nutrient absorption, their overall health and growth performance tend to experience positive effects. Probiotics can thus, through their actions on intestinal microbial composition, morpho-histological structure, and intestinal digestive and enzymatic activity, lead to improved weight gain, enhanced food utilization, and a reduction in the occurrence of digestive disorders. It is noteworthy that the efficacy of probiotics may be influenced by various factors, including fish species, specific probiotic strains utilized, dosage and duration of probiotic administration, and the environmental conditions of the fish rearing system.

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