

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

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 with a particular focus on tilapia, which has gained increased attention in recent research. Probiotics, live microorganisms administered at appropriate levels, can foster a balanced gut microbiota in animals. This can yield advantages like pathogen defence, improved digestion, enhanced growth, and increased survival rates in Tilapia. Probiotics are emerging as tools to promote healthy intestinal environments in Tilapia and other fish species, with potential to positively influence gut structure, ecosystem, growth, and disease resistance. The dynamic interplay between tilapia and their intestinal microbiota has garnered significant attention, affecting tilapia's health, performance, and overall well-being. This review compiles research findings on the influence of probiotics on tilapia intestinal ecosystems, morpho-histological structures, and enzymatic activities. It outlines their impact on gut microbiota composition in tilapia, demonstrating their ability to increase beneficial bacteria while reducing pathogenic strains. Probiotics can enhance intestinal morphology in tilapia, promoting villi development, goblet cell density, and mucous layer thickness. Additionally, they influence digestive enzyme activity in tilapia, resulting in improved nutrient absorption and tilapia growth. Although this field is continually evolving, the progress in deciphering probiotics' complex interactions with tilapia guts underscores their potential benefits in advancing tilapia aquaculture practices.

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 et al., 2023a). 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; Waiyamina 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; Jose et al., 2023; Syanya et al., 2023b). 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 fish intestinal environment and structure (figure 1) 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 with an accent put on tilapia which seemed to get attention on research. It will provide a comprehensive overview of this topic and predict future perspectives on the use of probiotics in aquaculture.

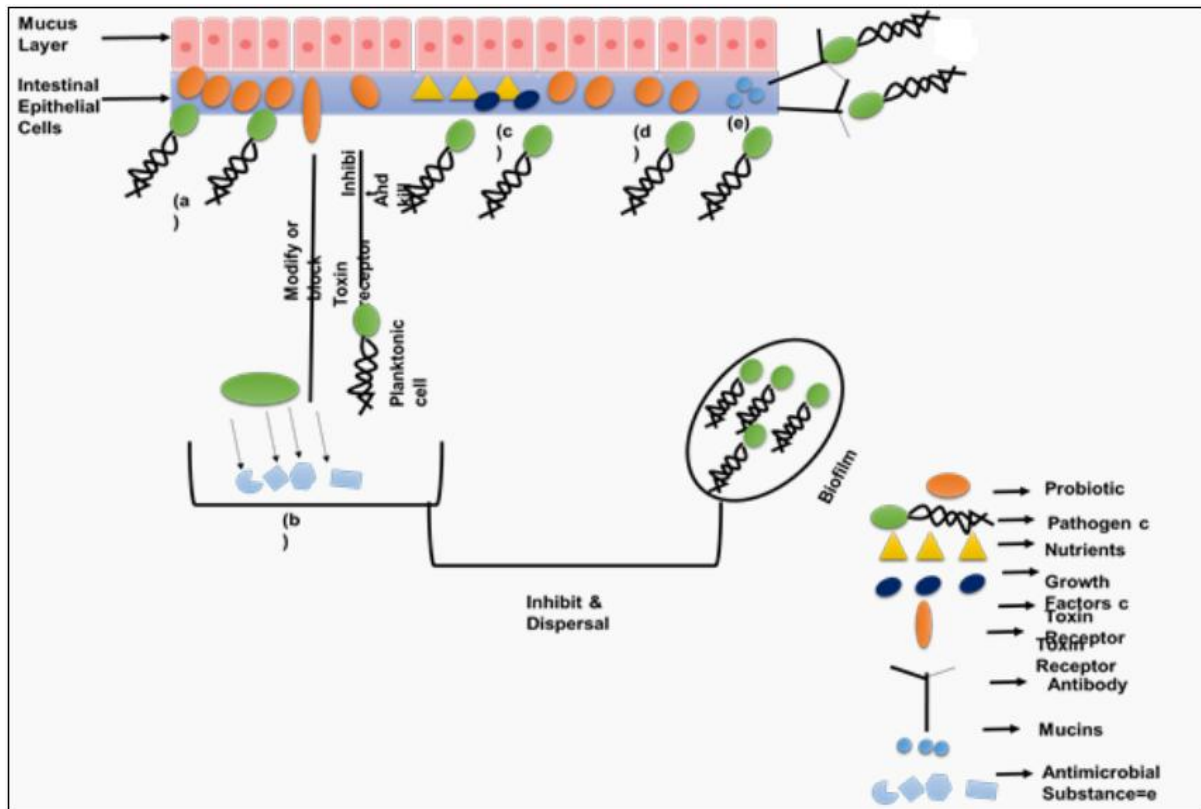


Figure 1: Some effects of probiotics on fish gut. Competition with pathogens on space (a), creation of antimicrobial substances (b), competition on nutrients, hormones and minerals (c), improvement of mucosal adhesion (d), enhancement of efficiency of the epithelial barrier (e). (Credit: Sharma et al. 2023)

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 (Science Direct), Springer Nature, Wiley, Taylor and Francis, and journal websites were consulted to gather a total of 136 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

Microbial interactions, ranging from beneficial to harmful, are fluid and influenced by environmental conditions. Host-microbe symbioses within microbial communities can involve multiple and diverse interactions, including cooperation and competition (Egan et al., 2020). Understanding these interplays is crucial, especially when examining their impact on fish gut microbiota (Figure 2). The fish gut microbiota plays a crucial role in digestion, nutrient absorption, immune system regulation, and overall health (Diwan et al., 2023; Ibrahim, 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; 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.

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 et al., 2020a). Additionally, multi-species probiotic supplementation in *Pangasianodon hypophthalmus* 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 *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 (Etyemez Büyükdeveci et al., 2023; 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 *B. 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 *Rummeliibacillus stabekisii* 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 *B. subtilis* and *B. 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 microecological 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.

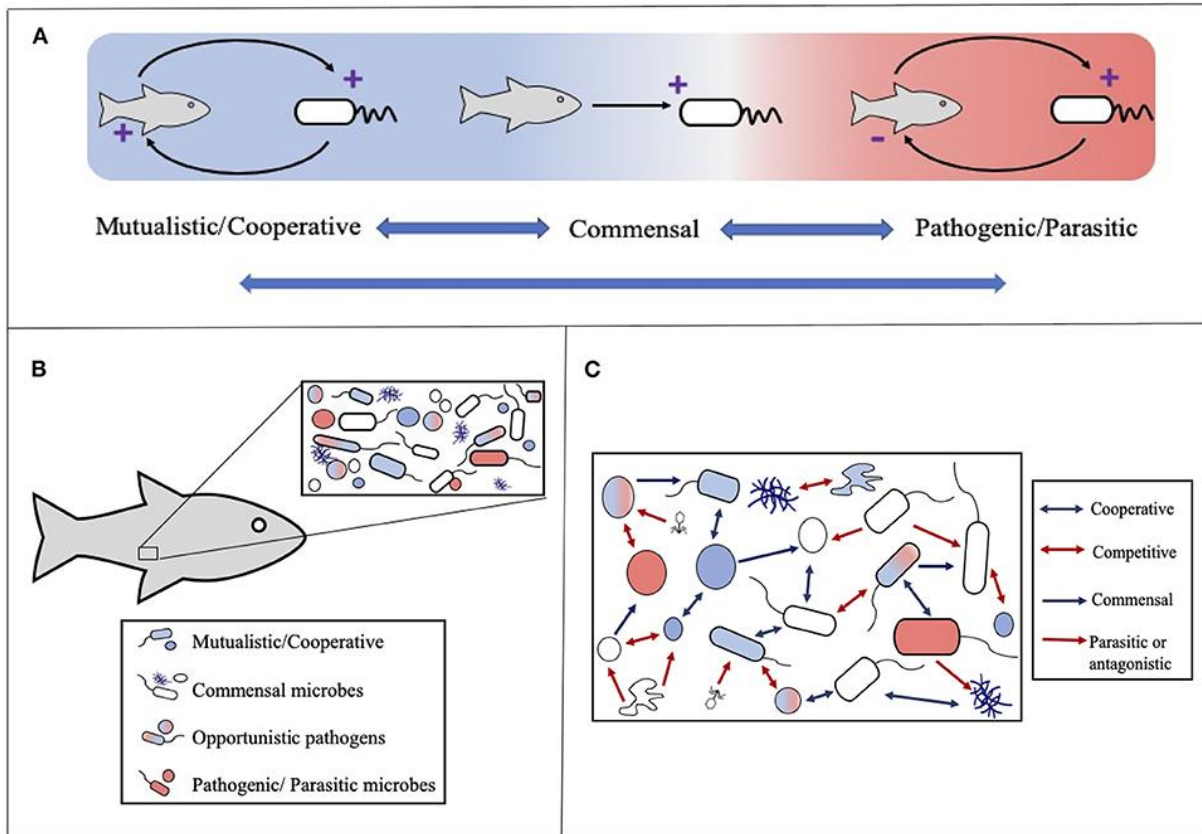


Figure 2: Microbial interactions in fish gut. They can change from mutual beneficial relation to harmful relation (A). Relations between host and microbes refers to its participation to different relations with microbial communities in its gut (B). Gut microbial communities are in different types of interrelations (C). (Credit: Egan et al. 2020).

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
<i>Bacillus subtilis</i> (+ malic acid)	Nile tilapia	Reduction of intestinal pH; decrease in the intestinal bacterial count	(Hassaan et al., 2018)
<i>Bacillus</i> species (TCMBS) + herbal	Nile tilapia	Significant increase in β -defensin and lysozyme	(Abarike et al., 2018)
<i>Bacillus subtilis</i> (endospores)	Nile tilapia	Positive regulation of gene expression of the two pro-inflammatory cytokines TNF- α and IL-1 β	(Galagarza et al., 2018)
<i>Lactobacillus rhamnosus</i> JCM1136 & <i>Lactococcus lactis</i> subsp. <i>lactis</i> JCM5805	Nile tilapia	Higher expression of immunity-related genes TNF- α , IFN- γ , lysozyme (lyzc), heat shock protein 70 (hsp70), and IL-1 β ; 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)
<i>Rummeliibacillus stabekisii</i>	Nile tilapia	Increase in the abundance of potential probiotics (<i>Bacillus</i> and <i>Lactobacillus</i> spp.); Reduction in the abundance of potential pathogenic bacteria (<i>Streptococcus</i> and <i>Staphylococcus</i> spp.); Significant increase in intestinal digestive enzymes protease, cellulase, and xylanase	(Tan et al., 2019)
<i>Bacillus velezensis</i> LF01	Nile tilapia	Significant increase in genes related to the immune system (C3, lysozyme c, and MHC-II β); Accumulation of more beneficial microorganisms; Inhibition of the growth of potentially pathogenic <i>Edwardsiella</i> and <i>Plesiomonas</i>	(D. Zhang et al., 2019)
<i>Lactococcus lactis</i> 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)
<i>Bacillus cereus</i> NY5, <i>Bacillus subtilis</i>	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
<i>Clostridium butyricum</i>	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)
<i>Bacillus amyloliquefaciens</i>	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)
<i>Bacillus subtilis</i> & <i>Enterococcus faecalis</i>	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)
<i>Clostridium autoethanogenum</i> (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 1 β (Pept 1 β), 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)
<i>Bacillus subtilis</i> & <i>Bacillus licheniformis</i>	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)
<i>Bacillus subtilis</i> spores	Nile tilapia	Increase in the relative abundance of Cetobacterium, Gemmobacter, and Bacillus.	(Deng et al., 2022b)
<i>Vibrio sp.</i> & <i>Bacillus cereus</i>	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
<i>Lactobacillus reuteri</i>	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 hif1 α , 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)
<i>Bacillus subtilis</i> & <i>Lactobacillus acidophilus</i>	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)
<i>Bacillus subtilis</i> var. <i>natto</i>	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)
<i>B. subtilis</i> , <i>B. licheniformis</i> & <i>B. pumilus</i>	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)
<i>Bacillus mojavensis</i> B191 & <i>Bacillus subtilis</i> MRS11	Nile tilapia	Increase in goblet cells, intestinal villus length, microvillus length, microvillus density, and perimeter ratio in the intestine	(Etyemez Büyükdeveci et al., 2023)
<i>B. amyloliquefaciens</i> , <i>B. subtilis</i> , <i>B. licheniformis</i> , <i>B. pumilus</i>	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

As a natural segue from the impact of probiotics on fish gut microbiota, it becomes evident that these beneficial microorganisms not only shape the microbial composition but also have notable effects on the structural aspects of the intestines, including villi height, cellular morphology, and goblet cell density.

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; 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 (Duangnumswang et al., 2021; Gyawali et al., 2023; Martini et al., 2017; Pelaseyed et al., 2014; S. Yang & Yu, 2021; Zheng et al., 2020).

Usually bacterial strains (Borges et al., 2020; Langlois et al., 2021; Li et al., 2019; 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; 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; 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; 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 (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; Li et al., 2021). For example, Chouayekh et al. (2023) demonstrated that the probiotic *B. 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 (*Misgurnus anguillicaudatus*) after 8 weeks of dietary supplementation (Yang et al., 2021). Similarly, in a 56-day experiment, the strains *Bacillus coagulans*, *B. licheniformis*, and *Paenibacillus polymyxa* significantly increased the height and width of intestinal villi in northern whiting (*Sillago sihama*) (Amoah et al., 2019). *Bacillus mojavensis* B191 and *Bacillus subtilis* MRS11 also can affect the structure of intestinal villi in Nile tilapia. In fact, (Etyemez Büyükdeveci et al., 2023) 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 (*Ctenopharyngodon idella*) 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-Bolivar et al., 2023; Mirabdollah Elahi 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; 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; 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, (Etyemez Büyükdeveci et al., 2023) showed that tilapia fed with a diet containing the probiotics *B. mojavensis* B191 and *B. 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 (*Mystus cavasius*). Similarly, *B. 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

Having explored how probiotics exert significant effects on the structural aspects of the intestines and mucosal health, we now delve into their multifaceted role in enhancing enzymatic and digestive activities, which ultimately contribute to improved nutrient absorption, growth, and overall health in fish.

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, *Rummeliibacillus stabekisii* 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 *B. 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 *B. 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 *B. 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 *B. 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 *B. licheniformis* HGA8B and *Paenibacillus polymyxa* HGA4C, which, when administered to Nile tilapia, significantly elevated both antioxidant and digestive enzymes in the intestine (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 enzyme types. For instance, activities of protease, amylase, catalase, superoxide dismutase, and lysozyme were notably enhanced through supplementation with *B. velezensis* GY65 in supplemented groups compared to control groups in mandarin fish (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 *B. licheniformis* and *B. subtilis* in Nile tilapia (Tachibana et al., 2021). Furthermore, dietary supplementation of Nile tilapia with *Lactobacillus plantarum* and *B. subtilis* stimulated specific amylase activity in the anterior intestine (Guimarães et al., 2021).

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 and recommendations

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. In aquaculture practice, the following conclusions and suggestions can be highlighted:

- In practical terms, by incorporating specific probiotics into fish feed, aquaculture operations can potentially reduce the incidence of diseases and improve the overall health of fish stocks.
- It is very important to select the right probiotic strains for specific fish species and environmental conditions. Aquaculture operators can use this knowledge to make informed choices about which probiotics to incorporate into their feed formulations.
- By incorporating probiotics that enhance specific enzyme activities, aquaculture producers can improve the digestibility of feed ingredients. This leads to more efficient nutrient utilization by fish, reducing feed wastage and production costs.
- With the implications for the management of aquaculture systems, especially those exposed to variable or challenging conditions, Probiotic supplementation can help fish better cope with stressors, improving their overall resilience.
- By improving nutrient absorption and reducing the need for antibiotics or other disease treatments, probiotics contribute to more sustainable aquaculture practices. This can lead to reduced environmental impact and an eco-friendlier approach to fish farming.
- Research on the effects of probiotics in Tilapia and other fish species should expand beyond examining the gut and encompass additional areas like the skin, gills, flesh quality (including nutrient, mineral, and elemental content), and the water conditions in which they are bred. Therefore, we strongly recommend conducting further studies that explore how probiotics influence a broader range of enzymes while considering the various factors that impact the activity of digestive enzymes in fish.

Competing interests

The authors declare no competing interests in relation to this study.

References

- Abarike, E. D., Jian, J., Tang, J., Cai, J., Yu, H., Lihua, C., & Jun, L. (2018). Influence of traditional Chinese medicine and *Bacillus* species (TCMBS) on growth, immune response and disease resistance in Nile tilapia, *Oreochromis niloticus*. *Aquaculture Research*, *49*(7), 2366–2375. <https://doi.org/10.1111/are.13691>
- Abdel-Latif, H. M. R., Chaklader, M. R., Shukry, M., Ahmed, H. A., & Khallaf, M. A. (2023). A multispecies probiotic modulates growth, digestive enzymes, immunity, hepatic antioxidant activity, and disease resistance of *Pangasianodon hypophthalmus* fingerlings. *Aquaculture*, *563*. <https://doi.org/10.1016/j.aquaculture.2022.738948>
- Ahmad, R., Yu, Y. H., Hsiao, F. S. H., Su, C. H., Liu, H. C., Tobin, I., Zhang, G., & Cheng, Y. H. (2022). Influence of Heat Stress on Poultry Growth Performance, Intestinal Inflammation, and Immune Function and Potential Mitigation by Probiotics. In *Animals* (Vol. 12, Issue 17). MDPI. <https://doi.org/10.3390/ani12172297>
- Ahmed, I., Li, Z., Shahzad, S., Naveed, S., Khan, A. K., Ahmed, A., Kamran, Z., Yousaf, M., Ahmad, S., Afzal, G., Ahmad, H. I., Yasin, N. A., Jia, J., Hussain, M., & Munir, S. (2022). Potential Probiotics Role in Excluding Antibiotic Resistance. In *Journal of Food Quality* (Vol. 2022). Hindawi Limited. <https://doi.org/10.1155/2022/5590004>
- Al-Hisnawi, A., Rodiles, A., Rawling, M. D., Castex, M., Waines, P., Gioacchini, G., Carnevali, O., & Merrifield, D. L. (2019). Dietary probiotic *Pediococcus acidilactici* MA18/5M modulates the intestinal microbiota and stimulates intestinal immunity in rainbow trout (*Oncorhynchus mykiss*). *Journal of the World Aquaculture Society*, *50*(6), 1133–1151. <https://doi.org/10.1111/jwas.12642>
- Al-Yassir, F., Khoder, G., Sugathan, S., Saseedharan, P., Al Menhali, A., & Karam, S. M. (2021). Modulation of stem cell progeny by probiotics during regeneration of gastric mucosal erosions. *Biology*, *10*(7). <https://doi.org/10.3390/biology10070596>
- Amoah, K., Huang, Q. C., Tan, B. P., Zhang, S., Chi, S. Y., Yang, Q. H., Liu, H. Y., & Dong, X. H. (2019). Dietary supplementation of probiotic *Bacillus coagulans* ATCC 7050, improves the growth performance, intestinal morphology, microflora, immune response, and disease confrontation of Pacific white shrimp, *Litopenaeus vannamei*. *Fish and Shellfish Immunology*, *87*, 796–808. <https://doi.org/10.1016/j.fsi.2019.02.029>
- Amoah, K., Tan, B., Zhang, S., Chi, S., Yang, Q., Liu, H., Yang, Y., Zhang, H., & Dong, X. (2023). Host gut-derived *Bacillus* probiotics supplementation improves growth performance, serum and liver immunity, gut health, and resistive capacity against *Vibrio harveyi* infection in hybrid grouper (*♀Epinephelus fuscoguttatus* × *♂E. lanceolatus*). *Animal Nutrition*. <https://doi.org/10.1016/j.aninu.2023.05.005>
- Assan, D., Kuebutornye, F. K. A., Hlordzi, V., Chen, H., Mraz, J., Mustapha, U. F., & Abarike, E. D. (2022). Effects of probiotics on digestive enzymes of fish (finfish and shellfish); status and prospects: a mini review. In *Comparative biochemistry and physiology. Part B, Biochemistry & molecular biology* (Vol. 257, p. 110653). NLM (Medline). <https://doi.org/10.1016/j.cbpb.2021.110653>
- Back, S. J., Park, S. J., Moon, J. S., Lee, S. B., Jo, S. J., Nam, T. J., Bai, S. C., Kong, I. S., Lee, K. J., Lee, B. J., Hur, S. W., Lee, S., & Choi, Y. H. (2020). The effects of dietary heat-killed probiotics bacteria

additives in low-fishmeal feed on growth performance, immune responses, and intestinal morphology in juvenile olive flounder *Paralichthys olivaceus*. *Aquaculture Reports*, 18. <https://doi.org/10.1016/j.aqrep.2020.100415>

- Bondad-Reantaso, M. G., MacKinnon, B., Karunasagar, I., Fridman, S., Alday-Sanz, V., Brun, E., Le Groumellec, M., Li, A., Surachetpong, W., Karunasagar, I., Hao, B., Dall'Occo, A., Urbani, R., & Caputo, A. (2023). Review of alternatives to antibiotic use in aquaculture. In *Reviews in Aquaculture*. John Wiley and Sons Inc. <https://doi.org/10.1111/raq.12786>
- Borges, N., Keller-Costa, T., Sanches-Fernandes, G. M. M., Louvado, A., Gomes, N. C. M., & Costa, R. (2020). *Annual Review of Animal Biosciences Bacteriome Structure, Function, and Probiotics in Fish Larviculture: The Good, the Bad, and the Gaps*. <https://doi.org/10.1146/annurev-animal-062920>
- Chen, P., Xu, T., Zhang, C., Tong, X., Shaukat, A., He, Y., Liu, K., & Huang, S. (2022). Effects of Probiotics and Gut Microbiota on Bone Metabolism in Chickens: A Review. In *Metabolites* (Vol. 12, Issue 10). MDPI. <https://doi.org/10.3390/metabo12101000>
- Chen, X., Xie, J., Liu, Z., Yin, P., Chen, M., Liu, Y., Tian, L., & Niu, J. (2020). Modulation of growth performance, non-specific immunity, intestinal morphology, the response to hypoxia stress and resistance to *Aeromonas hydrophila* of grass carp (*Ctenopharyngodon idella*) by dietary supplementation of a multi-strain probiotic. *Comparative Biochemistry and Physiology Part - C: Toxicology and Pharmacology*, 231. <https://doi.org/10.1016/j.cbpc.2020.108724>
- Chouayekh, H., Farhat-Khemakhem, A., Karray, F., Boubaker, I., Mhiri, N., Abdallah, M. Ben, Alghamdi, O. A., & Guerbej, H. (2023). Effects of Dietary Supplementation with *Bacillus amyloliquefaciens* US573 on Intestinal Morphology and Gut Microbiota of European Sea Bass. *Probiotics and Antimicrobial Proteins*, 15(1), 30–43. <https://doi.org/10.1007/s12602-022-09974-w>
- Dabbagh, A., Oraji, H., Amirkolaie, A. K., & Ansari, Z. (2021). Effect of *Lactobacillus plantarum* probiotic and different levels of soybean meal on growth and intestinal histomorphometry in rainbow trout diet. *Aquatic Animals Nutrition*, 7(4), 61–79. <https://doi.org/10.22124/janb.2022.22593.1173>
- Dawood, M. A. O., Magouz, F. I., Salem, M. F. I., & Abdel-Daim, H. A. (2019). Modulation of digestive enzyme activity, blood health, oxidative responses and growth-related gene expression in GIFT by heat-killed *Lactobacillus plantarum* (L-137). *Aquaculture*, 505, 127–136. <https://doi.org/10.1016/j.aquaculture.2019.02.053>
- Dawood, M. A. O., Magouz, F. I., Salem, M. F. I., Elbially, Z. I., & Abdel-Daim, H. A. (2020). Synergetic Effects of *Lactobacillus plantarum* and β -Glucan on Digestive Enzyme Activity, Intestinal Morphology, Growth, Fatty Acid, and Glucose-Related Gene Expression of Genetically Improved Farmed Tilapia. *Probiotics and Antimicrobial Proteins*, 12(2), 389–399. <https://doi.org/10.1007/s12602-019-09552-7>
- Deng, Y., Verdegem, M. C. J., Eding, E., & Kokou, F. (2022a). Effect of rearing systems and dietary probiotic supplementation on the growth and gut microbiota of Nile tilapia (*Oreochromis niloticus*) larvae. *Aquaculture*, 546. <https://doi.org/10.1016/j.aquaculture.2021.737297>
- Deng, Y., Verdegem, M. C. J., Eding, E., & Kokou, F. (2022b). Effect of rearing systems and dietary probiotic supplementation on the growth and gut microbiota of Nile tilapia (*Oreochromis niloticus*) larvae. *Aquaculture*, 546. <https://doi.org/10.1016/j.aquaculture.2021.737297>

- Dhillon, O., & Bhatnagar, A. (2020). *Gut colonization and permanence of the probiotics in Labeo calbasu (Hamilton, 1822)* (Vol. 24, Issue 7). www.ejabf.journals.ekb.eg
- Diwan, A. D., Harke, S. N., Gopalkrishna, & Panche, A. N. (2022). Aquaculture industry prospective from gut microbiome of fish and shellfish: An overview. In *Journal of Animal Physiology and Animal Nutrition* (Vol. 106, Issue 2, pp. 441–469). John Wiley and Sons Inc. <https://doi.org/10.1111/jpn.13619>
- Diwan, A. D., Harke, S. N., & Panche, A. N. (2023). Host-microbiome interaction in fish and shellfish: An overview. In *Fish and Shellfish Immunology Reports* (Vol. 4). Elsevier Ltd. <https://doi.org/10.1016/j.fsirep.2023.100091>
- Du, R. Y., Zhang, H. Q., Chen, J. X., Zhu, J., He, J. Y., Luo, L., Lin, S. M., & Chen, Y. J. (2021). Effects of dietary *Bacillus subtilis* DSM 32315 supplementation on the growth, immunity and intestinal morphology, microbiota and inflammatory response of juvenile largemouth bass *Micropterus salmoides*. *Aquaculture Nutrition*, 27(6), 2119–2131. <https://doi.org/10.1111/anu.13347>
- Duangnumswang, Y., Zentek, J., & Goodarzi Boroojeni, F. (2021). Development and Functional Properties of Intestinal Mucus Layer in Poultry. In *Frontiers in Immunology* (Vol. 12). Frontiers Media S.A. <https://doi.org/10.3389/fimmu.2021.745849>
- Egan, S., Fukatsu, T., & Francino, M. P. (2020). Opportunities and Challenges to Microbial Symbiosis Research in the Microbiome Era. *Frontiers in Microbiology*, 11. <https://doi.org/10.3389/fmicb.2020.01150>
- Egerton, S., Culloty, S., Whooley, J., Stanton, C., & Ross, R. P. (2018). The gut microbiota of marine fish. In *Frontiers in Microbiology* (Vol. 9, Issue MAY). Frontiers Media S.A. <https://doi.org/10.3389/fmicb.2018.00873>
- El-Saadony, M. T., Alagawany, M., Patra, A. K., Kar, I., Tiwari, R., Dawood, M. A. O., Dhama, K., & Abdel-Latif, H. M. R. (2021). The functionality of probiotics in aquaculture: An overview. In *Fish and Shellfish Immunology* (Vol. 117, pp. 36–52). Academic Press. <https://doi.org/10.1016/j.fsi.2021.07.007>
- Elsabagh, M., Mohamed, R., Moustafa, E. M., Hamza, A., Farrag, F., Decamp, O., Dawood, M. A. O., & Eltholth, M. (2018). Assessing the impact of *Bacillus* strains mixture probiotic on water quality, growth performance, blood profile and intestinal morphology of Nile tilapia, *Oreochromis niloticus*. *Aquaculture Nutrition*, 24(6), 1613–1622. <https://doi.org/10.1111/anu.12797>
- Enferadi, M. H. N., Mohammadzadeh, F., Soltani, M., Bahri, A. H., & Sheikhzadeh, N. (2018). Effects of *Lactobacillus plantarum* on growth performance, proteolytic enzymes activity and intestine morphology in rainbow trout (*Oncorhynchus mykiss*). *Turkish Journal of Fisheries and Aquatic Sciences*, 18(2), 351–356. https://doi.org/10.4194/1303-2712-v18_2_14
- Etyemez Büyükdeveci, M., Cengizler, İ., Balcázar, J. L., & Demirkale, İ. (2023). Effects of two host-associated probiotics *Bacillus mojavensis* B191 and *Bacillus subtilis* MRS11 on growth performance, intestinal morphology, expression of immune-related genes and disease resistance of Nile tilapia (*Oreochromis niloticus*) against *Streptococcus iniae*. *Developmental and Comparative Immunology*, 138. <https://doi.org/10.1016/j.dci.2022.104553>
- Fei, H., Lin, G. dong, Zheng, C. cai, Huang, M. meng, Qian, S. C., Wu, Z. ju, Sun, C., Shi, Z. guang, Li, J. you, & Han, B. nan. (2018). Effects of *Bacillus amyloliquefaciens* and *Yarrowia lipolytica* lipase 2

- on immunology and growth performance of Hybrid sturgeon. *Fish and Shellfish Immunology*, 82, 250–257. <https://doi.org/10.1016/j.fsi.2018.08.031>
- Fijan, S. (2014). Microorganisms with claimed probiotic properties: An overview of recent literature. In *International Journal of Environmental Research and Public Health* (Vol. 11, Issue 5, pp. 4745–4767). MDPI. <https://doi.org/10.3390/ijerph110504745>
- Foucault, P., Gallet, A., Duval, C., Marie, B., & Duperron, S. (2022). Gut microbiota and holobiont metabolome composition of the medaka fish (*Oryzias latipes*) are affected by a short exposure to the cyanobacterium *Microcystis aeruginosa*. *Aquatic Toxicology (Amsterdam, Netherlands)*, 253, 106329. <https://doi.org/10.1016/j.aquatox.2022.106329>
- Foyosal, M. J., Nguyen, T. T. T., Chaklader, M. R., Siddik, M. A. B., Tay, C. Y., Fotedar, R., & Gupta, S. K. (2019). Marked variations in gut microbiota and some innate immune responses of fresh water crayfish, marron (*Cherax cainii*, Austin 2002) fed dietary supplementation of *Clostridium butyricum*. *PeerJ*, 2019(8). <https://doi.org/10.7717/peerj.7553>
- Gaffar, M. A., Zaman, M. K., Islam, M. S., Islam, M., Hossain, M. K., Shahriar, S. I. M., & Shahjahan, M. (2023). Effects of probiotics on growth, survival, and intestinal and liver morphometry of Gangetic mystus (*Mystus cavasius*). *Saudi Journal of Biological Sciences*, 30(7). <https://doi.org/10.1016/j.sjbs.2023.103683>
- Galagarza, O. A., Smith, S. A., Drahos, D. J., Eifert, J. D., Williams, R. C., & Kuhn, D. D. (2018). Modulation of innate immunity in Nile tilapia (*Oreochromis niloticus*) by dietary supplementation of *Bacillus subtilis* endospores. *Fish and Shellfish Immunology*, 83, 171–179. <https://doi.org/10.1016/j.fsi.2018.08.062>
- Gallo, B. D., Farrell, J. M., & Leydet, B. F. (2020). Fish Gut Microbiome: A Primer to an Emerging Discipline in the Fisheries Sciences. *Fisheries*, 45(5), 271–282. <https://doi.org/10.1002/fsh.10379>
- Ghalwash, H. R., Salah, A. S., El-Nokrashy, A. M., Abozeid, A. M., Zaki, V. H., & Mohamed, R. A. (2022). Dietary supplementation with *Bacillus* species improves growth, intestinal histomorphology, innate immunity, antioxidative status and expression of growth and appetite-regulating genes of Nile tilapia fingerlings. *Aquaculture Research*, 53(4), 1378–1394. <https://doi.org/10.1111/are.15671>
- Ghori, I., Tabassum, M., Ahmad, T., Zuberi, A., & Imran, M. (2018). *Geotrichum candidum* enhanced the *Enterococcus faecium* impact in improving physiology, and health of *Labeo rohita* (Hamilton, 1822) by modulating gut microbiome under mimic aquaculture conditions. *Turkish Journal of Fisheries and Aquatic Sciences*, 18(11), 1255–1267. https://doi.org/10.4194/1303-2712-v18_11_02
- Ghori, I., Tubassam, M., Ahmad, T., Zuberi, A., & Imran, M. (2022). Gut microbiome modulation mediated by probiotics: Positive impact on growth and health status of *Labeo rohita*. *Frontiers in Physiology*, 13. <https://doi.org/10.3389/fphys.2022.949559>
- Giri, S. S., Jun, J. W., Yun, S., Kim, H. J., Kim, S. G., Kang, J. W., Kim, S. W., Han, S. J., Park, S. C., & Sukumaran, V. (2019). Characterisation of Lactic Acid Bacteria Isolated from the Gut of *Cyprinus carpio* That May Be Effective Against Lead Toxicity. *Probiotics and Antimicrobial Proteins*, 11(1), 65–73. <https://doi.org/10.1007/s12602-017-9367-6>

- Giri, S. S., Yun, S., Jun, J. W., Kim, H. J., Kim, S. G., Kang, J. W., Kim, S. W., Han, S. J., Sukumaran, V., & Park, S. C. (2018). Therapeutic effect of intestinal autochthonous *Lactobacillus reuteri* P16 against waterborne lead toxicity in *Cyprinus carpio*. *Frontiers in Immunology*, *9*(AUG). <https://doi.org/10.3389/fimmu.2018.01824>
- González-Félix, M. L., Gatlin, D. M., Urquidez-Bejarano, P., de la Reé-Rodríguez, C., Duarte-Rodríguez, L., Sánchez, F., Casas-Reyes, A., Yamamoto, F. Y., Ochoa-Leyva, A., & Perez-Velazquez, M. (2018). Effects of commercial dietary prebiotic and probiotic supplements on growth, innate immune responses, and intestinal microbiota and histology of *Totoaba macdonaldi*. *Aquaculture*, *491*, 239–251. <https://doi.org/10.1016/j.aquaculture.2018.03.031>
- Guimarães, M. C., da Silva Guimarães, A. I. C., Natori, M. M., Alarcon, M. F. F., Dias, D. de C., Ishikawa, C. M., Tapia-Paniagua, S., Moriñigo, M. Á., Moyano, F. J., & Tachibana, L. (2021). Oral administration of *Bacillus subtilis* and *Lactobacillus plantarum* modulates the gut microbiota and increases the amylase activity of Nile tilapia (*Oreochromis niloticus*). *Aquaculture International*, *29*(1), 91–104. <https://doi.org/10.1007/s10499-020-00612-2>
- Gyawali, I., Zhou, G., Xu, G., Li, G., Wang, Y., Zeng, Y., Li, J., Zhou, J., Zhu, C., Shu, G., & Jiang, Q. (2023). Supplementation of microencapsulated probiotics modulates gut health and intestinal microbiota. *Food Science and Nutrition*. <https://doi.org/10.1002/fsn3.3414>
- Haque, M. M., Hasan, N. A., Eltholth, M. M., Saha, P., Mely, S. S., Rahman, T., & Murray, F. J. (2021). Assessing the impacts of in-feed probiotic on the growth performance and health condition of pangasius (*Pangasianodon hypophthalmus*) in a farm trial. *Aquaculture Reports*, *20*. <https://doi.org/10.1016/j.aqrep.2021.100699>
- Haraz, Y. G., Shourbela, R. M., El-Hawarry, W. N., Mansour, A. M., & Elblehi, S. S. (2023). Performance of juvenile *Oreochromis niloticus* (Nile tilapia) raised in conventional and biofloc technology systems as influenced by probiotic water supplementation. *Aquaculture*, *566*. <https://doi.org/10.1016/j.aquaculture.2022.739180>
- Hasan, I., Rimoldi, S., Saroglia, G., & Terova, G. (2023). Sustainable Fish Feeds with Insects and Probiotics Positively Affect Freshwater and Marine Fish Gut Microbiota. In *Animals* (Vol. 13, Issue 10). MDPI. <https://doi.org/10.3390/ani13101633>
- Hassaan, M. S., Soltan, M. A., Jarmolowicz, S., & Abdo, H. S. (2018). Combined effects of dietary malic acid and *Bacillus subtilis* on growth, gut microbiota and blood parameters of Nile tilapia (*Oreochromis niloticus*). *Aquaculture Nutrition*, *24*(1), 83–93. <https://doi.org/10.1111/anu.12536>
- Hortillosa, E. M., Amar, M. J. A., Nuñal, S. N., Pedroso, F. L., & Ferriols, V. M. E. N. (2022). Effects of putative dietary probiotics from the gut of milkfish (*Chanos chanos*) on the growth performance and intestinal enzymatic activities of juvenile Nile tilapia (*Oreochromis niloticus*). *Aquaculture Research*, *53*(1), 98–108. <https://doi.org/10.1111/are.15556>
- Hossain, M. K., Hossain, M. M., Mim, Z. T., Khatun, H., Hossain, M. T., & Shahjahan, M. (2022). Multi-species probiotics improve growth, intestinal microbiota and morphology of Indian major carp mrigal *Cirrhinus cirrhosus*. *Saudi Journal of Biological Sciences*, *29*(9). <https://doi.org/10.1016/j.sjbs.2022.103399>

- Ibrahem, M. D. (2013). Evolution of probiotics in aquatic world: Potential effects, the current status in Egypt and recent prospectives. In *Journal of Advanced Research* (Vol. 6, Issue 6, pp. 765–791). Elsevier. <https://doi.org/10.1016/j.jare.2013.12.004>
- Islam, S. M. M., Rohani, M. F., & Shahjahan, M. (2021). Probiotic yeast enhances growth performance of Nile tilapia (*Oreochromis niloticus*) through morphological modifications of intestine. *Aquaculture Reports*, 21. <https://doi.org/10.1016/j.aqrep.2021.100800>
- Jahan, N., Islam, S. M. M., Rohani, M. F., Hossain, M. T., & Shahjahan, M. (2021). Probiotic yeast enhances growth performance of rohu (*Labeo rohita*) through upgrading hematology, and intestinal microbiota and morphology. *Aquaculture*, 545. <https://doi.org/10.1016/j.aquaculture.2021.737243>
- Jaramillo-Torres, A., Rawling, M. D., Rodiles, A., Mikalsen, H. E., Johansen, L. H., Tinsley, J., Forberg, T., Aasum, E., Castex, M., & Merrifield, D. L. (2019). Influence of dietary supplementation of probiotic *pediococcus acidilactici* MA18/5M during the transition from freshwater to seawater on intestinal health and microbiota of atlantic salmon (*Salmo salar* L.). *Frontiers in Microbiology*, 10(SEP). <https://doi.org/10.3389/fmicb.2019.02243>
- Jayaprakash, S., & Parvathi, K. (2019). Influences of Isolated Gut Probiotics *Bacillus subtilis* on Intestinal histological Changes in the Freshwater fish *Labeo rohita* (Hamilton, 1822) fingerlings. *laetsd Journal for Advanced Research in Applied Sciences*, 6(6).
- Jha, R., Das, R., Oak, S., & Mishra, P. (2020). Probiotics (Direct-fed microbials) in poultry nutrition and their effects on nutrient utilization, growth and laying performance, and gut health: A systematic review. In *Animals* (Vol. 10, Issue 10, pp. 1–19). MDPI AG. <https://doi.org/10.3390/ani10101863>
- Jiang, L., Zhou, X., Yu, J., Bao, S., Li, J., Wu, Q., Wu, M., Wang, Y., & Liu, B. (2022). Fermented tea residue improved growth performance, liver antioxidant capacity, intestinal morphology and resistance to *Aeromonas hydrophila* infection in juvenile largemouth bass (*Micropterus salmoides*). *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.999947>
- Jose, M. S., Arun, D., Neethu, S., Radhakrishnan, E. K., & Jyothis, M. (2023). Probiotic *Paenibacillus polymyxa* HGA4C and *Bacillus licheniformis* HGA8B combination improved growth performance, enzymatic profile, gene expression and disease resistance in *Oreochromis niloticus*. *Microbial Pathogenesis*, 174, 105951. <https://doi.org/10.1016/j.micpath.2022.105951>
- Kong, Y., Li, M., Chu, G., Liu, H., Shan, X., Wang, G., & Han, G. (2021). The positive effects of single or conjoint administration of lactic acid bacteria on *Channa argus*: Digestive enzyme activity, antioxidant capacity, intestinal microbiota and morphology. *Aquaculture*, 531. <https://doi.org/10.1016/j.aquaculture.2020.735852>
- Kuebutornye, F. K. A., Abarike, E. D., & Lu, Y. (2019). A review on the application of *Bacillus* as probiotics in aquaculture. In *Fish and Shellfish Immunology* (Vol. 87, pp. 820–828). Academic Press. <https://doi.org/10.1016/j.fsi.2019.02.010>
- Kuebutornye, F. K. A., Wang, Z., Lu, Y., Abarike, E. D., Sakyi, M. E., Li, Y., Xie, C. X., & Hlordzi, V. (2020). Effects of three host-associated *Bacillus* species on mucosal immunity and gut health of Nile tilapia, *Oreochromis niloticus* and its resistance against *Aeromonas hydrophila* infection. *Fish and Shellfish Immunology*, 97, 83–95. <https://doi.org/10.1016/j.fsi.2019.12.046>

- Laice, L. M., Corrêa Filho, R. A. C., Ventura, A. S., Farias, K. N. N., Silva, A. L. do N., Fernandes, C. E., Silva, A. C. F., Barbosa, P. T. L., de Souza, A. I., Emerenciano, M. G. C., & Povh, J. A. (2021). Use of symbiotics in biofloc (BFT)-based Nile tilapia culture: Production performance, intestinal morphometry and hematological parameters. *Aquaculture*, 530. <https://doi.org/10.1016/j.aquaculture.2020.735715>
- Lalitha, N., Ronald, B. S. M., Chitra, M. A., Hemalatha, S., Senthilkumar, T. M. A., & Muralidhar, M. (2022). Characterization of Lactic Acid Bacteria from the Gut of *Penaeus vannamei* as Potential Probiotic. *Indian Journal of Animal Research*, Of. <https://doi.org/10.18805/ijar.b-4983>
- Langlois, L., Akhtar, N., Tam, K. C., Dixon, B., & Reid, G. (2021). Fishing for the right probiotic: Host-microbe interactions at the interface of effective aquaculture strategies. In *FEMS Microbiology Reviews* (Vol. 45, Issue 6). Oxford University Press. <https://doi.org/10.1093/femsre/fuab030>
- Lertwanakarn, T., Trongwongsa, P., Yingsakmongkol, S., Khemthong, M., Tattiyapong, P., & Surachetpong, W. (2021). Antiviral activity of ribavirin against tilapia tilapinevirus in fish cells. *Pathogens*, 10(12). <https://doi.org/10.3390/pathogens10121616>
- Li, H. dong, Tian, X. li, & Dong, S. lin. (2019). Growth performance, non-specific immunity, intestinal histology and disease resistance of *Litopenaeus vannamei* fed on a diet supplemented with live cells of *Clostridium butyricum*. *Aquaculture*, 498, 470–481. <https://doi.org/10.1016/j.aquaculture.2018.09.003>
- Li, W., Huang, X., Lu, X., Jiang, B., Liu, C., Huang, Y., & Su, Y. (2022). Effects of dietary *Lactobacillus reuteri* on growth performance, nutrient retention, gut health and microbiota of the Nile tilapia (*Oreochromis niloticus*). *Aquaculture Reports*, 26. <https://doi.org/10.1016/j.aqrep.2022.101275>
- Li, W., Liu, B., Liu, Z., Yin, Y., Xu, G., Han, M., & Xie, L. (2021). Effect of dietary histamine on intestinal morphology, inflammatory status, and gut microbiota in yellow catfish (*Pelteobagrus fulvidraco*). *Fish and Shellfish Immunology*, 117, 95–103. <https://doi.org/10.1016/j.fsi.2021.07.017>
- Li, Z., Lu, T., Li, M., Mortimer, M., & Guo, L. H. (2023). Direct and gut microbiota-mediated toxicities of environmental antibiotics to fish and aquatic invertebrates. In *Chemosphere* (Vol. 329). Elsevier Ltd. <https://doi.org/10.1016/j.chemosphere.2023.138692>
- Liang, F., Li, C., Hou, T., Wen, C., Kong, S., Ma, D., Sun, C., & Li, S. (2020). Effects of Chitosan–gentamicin conjugate supplement on non-specific immunity, aquaculture water, intestinal histology and microbiota of pacific white shrimp (*litopenaeus vannamei*). *Marine Drugs*, 18(8). <https://doi.org/10.3390/MD18080419>
- Lin, S. M., Zhou, X. M., Zhou, Y. L., Kuang, W. M., Chen, Y. J., Luo, L., & Dai, F. Y. (2020). Intestinal morphology, immunity and microbiota response to dietary fibers in largemouth bass, *Micropterus salmoide*. *Fish and Shellfish Immunology*, 103, 135–142. <https://doi.org/10.1016/j.fsi.2020.04.070>
- Liu, Q., Wen, L., Pan, X., Huang, Y., Du, X., Qin, J., Zhou, K., Wei, Z., Chen, Z., Ma, H., Hu, T., & Lin, Y. (2021). Dietary supplementation of *Bacillus subtilis* and *Enterococcus faecalis* can effectively improve the growth performance, immunity, and resistance of tilapia against *Streptococcus agalactiae*. *Aquaculture Nutrition*, 27(4), 1160–1172. <https://doi.org/10.1111/anu.13256>

- Luan, Y., Li, M., Zhou, W., Yao, Y., Yang, Y., Zhang, Z., Ringø, E., Erik Olsen, R., Liu Clarke, J., Xie, S., Mai, K., Ran, C., & Zhou, Z. (2023). The Fish Microbiota: Research Progress and Potential Applications. In *Engineering*. Elsevier Ltd. <https://doi.org/10.1016/j.eng.2022.12.011>
- Maas, R. M., Deng, Y., Dersjant-Li, Y., Petit, J., Verdegem, M. C. J., Schrama, J. W., & Kokou, F. (2021). Exogenous enzymes and probiotics alter digestion kinetics, volatile fatty acid content and microbial interactions in the gut of Nile tilapia. *Scientific Reports*, *11*(1). <https://doi.org/10.1038/s41598-021-87408-3>
- Martini, E., Krug, S. M., Siegmund, B., Neurath, M. F., & Becker, C. (2017). Mend Your Fences: The Epithelial Barrier and its Relationship With Mucosal Immunity in Inflammatory Bowel Disease. In *CMGH* (Vol. 4, Issue 1, pp. 33–46). Elsevier Inc. <https://doi.org/10.1016/j.jcmgh.2017.03.007>
- Maulu, S., Hualiang, L., Ke, J., Ren, M., Ge, X., Huang, D., & Yu, H. (2021). Dietary Clostridium autoethanogenum protein modulates intestinal absorption, antioxidant status, and immune response in GIFT (*Oreochromis niloticus*) juveniles. *Aquaculture Research*, *52*(11), 5787–5799. <https://doi.org/10.1111/are.15454>
- Melo-Bolívar, J. F., Ruiz Pardo, R. Y., Hume, M. E., & Villamil Díaz, L. M. (2021). Multistrain probiotics use in main commercially cultured freshwater fish: a systematic review of evidence. In *Reviews in Aquaculture* (Vol. 13, Issue 4, pp. 1758–1780). John Wiley and Sons Inc. <https://doi.org/10.1111/raq.12543>
- Melo-Bolívar, J. F., Ruiz-Pardo, R. Y., Quintanilla Carvajal, M. X., Díaz, L. E., Alzate, J. F., Junca, H., Rodríguez Orjuela, J. A., & Villamil Diaz, L. M. (2023). Evaluation of dietary single probiotic isolates and probiotic multistrain consortia in growth performance, gut histology, gut microbiota, immune regulation, and infection resistance of Nile tilapia, *Oreochromis niloticus*, shows superior monostrain performance. *Fish & Shellfish Immunology*, 108928. <https://doi.org/10.1016/j.fsi.2023.108928>
- Mirabdollah Elahi, S. S., Mirnejad, R., Kazempoor, R., & Sotoodehnejadnematalahi, F. (2020). Study of the Histopathologic Effects of Probiotic Lactobacillus acidophilus in Exposure to E. coli O157: H7 in Zebrafish Intestine. *Iranian Red Crescent Medical Journal*, *22*(4). <https://doi.org/10.5812/ircmj.99400>
- Monzón-Atienza, L., Bravo, J., Serradell, A., Montero, D., Gómez-Mercader, A., & Acosta, F. (2023). Current Status of Probiotics in European Sea Bass Aquaculture as One Important Mediterranean and Atlantic Commercial Species: A Review. In *Animals* (Vol. 13, Issue 14). Multidisciplinary Digital Publishing Institute (MDPI). <https://doi.org/10.3390/ani13142369>
- Ngamkala, S., Satchasataporn, K., Setthawongsin, C., & Raksajit, W. (2020). Histopathological study and intestinal mucous cell responses against *Aeromonas hydrophila* in Nile tilapia administered with *Lactobacillus rhamnosus* GG. *Veterinary World*, *13*(5), 967–974. <https://doi.org/10.14202/vetworld.2020.967-974>
- Nikiforov-Nikishin, A., Nikiforov-Nikishin, D., Kochetkov, N., Smorodinskaya, S., & Klimov, V. (2022). The influence of probiotics of different microbiological composition on histology of the gastrointestinal tract of juvenile *Oncorhynchus mykiss*. *Microscopy Research and Technique*, *85*(2), 538–547. <https://doi.org/10.1002/jemt.23927>
- Nikiforov-Nikishin, D., Kochetkov, N., Klimov, V., & Bugaev, O. (2022). Effects of chelated complexes and probiotics on histological and morphometric parameters of the gastrointestinal tract of

juvenile carp (*Cyprinus carpio*). *New Zealand Journal of Zoology*.
<https://doi.org/10.1080/03014223.2022.2082495>

- Nimalan, N., Sørensen, S. L., Fečkaninová, A., Koščová, J., Mudroňová, D., Gancarčíková, S., Vatsos, I. N., Bisa, S., Kiron, V., & Sørensen, M. (2022). Mucosal barrier status in Atlantic salmon fed marine or plant-based diets supplemented with probiotics. *Aquaculture*, 547.
<https://doi.org/10.1016/j.aquaculture.2021.737516>
- Nimalan, N., Sørensen, S. L., Fečkaninová, A., Koščová, J., Mudroňová, D., Gancarčíková, S., Vatsos, I. N., Bisa, S., Kiron, V., & Sørensen, M. (2023). Supplementation of lactic acid bacteria has positive effects on the mucosal health of Atlantic salmon (*Salmo salar*) fed soybean meal. *Aquaculture Reports*, 28. <https://doi.org/10.1016/j.aqrep.2022.101461>
- Obianwuna, U. E., Agbai Kalu, N., Wang, J., Zhang, H., Qi, G., Qiu, K., & Wu, S. (2023). Recent Trends on Mitigative Effect of Probiotics on Oxidative-Stress-Induced Gut Dysfunction in Broilers under Necrotic Enteritis Challenge: A Review. In *Antioxidants* (Vol. 12, Issue 4). MDPI.
<https://doi.org/10.3390/antiox12040911>
- Oliveira, F. C., Kasai, R. Y. D., Fernandes, C. E., Souza da Silva, W., & de Campos, C. M. (2022). Probiotic, prebiotic and synbiotics supplementation on growth performance and intestinal histomorphometry *Pseudoplatystoma reticulatum* larvae. *Journal of Applied Aquaculture*, 34(2), 279–293. <https://doi.org/10.1080/10454438.2020.1841060>
- Pan, P. K., Wang, K. T., Wu, T. M., Chen, Y. Y., Nan, F. H., & Wu, Y. S. (2023). Heat inactive *Bacillus subtilis* var. natto regulate Nile tilapia (*Oreochromis niloticus*) intestine microbiota and metabolites involved in the intestine phagosome response. *Fish and Shellfish Immunology*, 134.
<https://doi.org/10.1016/j.fsi.2023.108567>
- Pelaseyed, T., Bergström, J. H., Gustafsson, J. K., Ermund, A., Birchenough, G. M. H., Schütte, A., van der Post, S., Svensson, F., Rodríguez-Piñeiro, A. M., Nyström, E. E. L., Wising, C., Johansson, M. E. V., & Hansson, G. C. (2014). The mucus and mucins of the goblet cells and enterocytes provide the first defense line of the gastrointestinal tract and interact with the immune system. In *Immunological Reviews* (Vol. 260, Issue 1, pp. 8–20). Blackwell Publishing Ltd.
<https://doi.org/10.1111/imr.12182>
- Pillinger, M., Weber, B., Standen, B., Schmid, M. C., & Kesselring, J. C. (2022). Multi-strain probiotics show increased protection of intestinal epithelial cells against pathogens in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, 560. <https://doi.org/10.1016/j.aquaculture.2022.738487>
- Poolsawat, L., Li, X., He, M., Ji, D., & Leng, X. (2020). *Clostridium butyricum* as probiotic for promoting growth performance, feed utilization, gut health and microbiota community of tilapia (*Oreochromis niloticus* × *O. aureus*). *Aquaculture Nutrition*, 26(3), 657–670.
<https://doi.org/10.1111/anu.13025>
- Qin, L., Xiang, J., Xiong, F., Wang, G., Zou, H., Li, W., Li, M., & Wu, S. (2020). Effects of *Bacillus licheniformis* on the growth, antioxidant capacity, intestinal barrier and disease resistance of grass carp (*Ctenopharyngodon idella*). *Fish and Shellfish Immunology*, 97, 344–350.
<https://doi.org/10.1016/j.fsi.2019.12.040>
- Reyes-Becerril, M., Alamillo, E., & Angulo, C. (2021). Probiotic and Immunomodulatory Activity of Marine Yeast *Yarrowia lipolytica* Strains and Response Against *Vibrio parahaemolyticus* in Fish.

Probiotics and Antimicrobial Proteins, 13(5), 1292–1305. <https://doi.org/10.1007/s12602-021-09769-5>

- Ringø, E., Harikrishnan, R., Soltani, M., & Ghosh, K. (2022). The Effect of Gut Microbiota and Probiotics on Metabolism in Fish and Shrimp. In *Animals* (Vol. 12, Issue 21). MDPI. <https://doi.org/10.3390/ani12213016>
- Ringø, E., Zhou, Z., Vecino, J. L. G., Wadsworth, S., Romero, J., Krogdahl, Olsen, R. E., Dimitroglou, A., Foey, A., Davies, S., Owen, M., Lauzon, H. L., Martinsen, L. L., De Schryver, P., Bossier, P., Sperstad, S., & Merrifield, D. L. (2016). Effect of dietary components on the gut microbiota of aquatic animals. A never-ending story? *Aquaculture Nutrition*, 22(2), 219–282. <https://doi.org/10.1111/anu.12346>
- Shang, X., Yu, P., Yin, Y., Zhang, Y., Lu, Y., Mao, Q., & Li, Y. (2021). Effect of selenium-rich *Bacillus subtilis* against mercury-induced intestinal damage repair and oxidative stress in common carp. *Comparative Biochemistry and Physiology Part - C: Toxicology and Pharmacology*, 239. <https://doi.org/10.1016/j.cbpc.2020.108851>
- Sharma, S. R., Parveen, S., & Singh, J. (2023). Exploración del potencial de los probióticos como agente de biocontrol. *Salud, Ciencia y Tecnología*, 3, 409. <https://doi.org/10.56294/saludcyt2023409>
- Siddik, M. A. B., Foysal, M. J., Fotedar, R., Francis, D. S., & Gupta, S. K. (2021). Probiotic yeast *Saccharomyces cerevisiae* coupled with *Lactobacillus casei* modulates physiological performance and promotes gut microbiota in juvenile barramundi, *Lates calcarifer*. *Aquaculture*, 546. <https://doi.org/10.1016/j.aquaculture.2021.737346>
- Spirina, E., Romanova, E., Romanov, V., Lyubomirova, V., Shadyeva, L., Shlenkina, T., & Rakova, L. (2019). Pathology of cells and tissues of the gastrointestinal tract of African catfish in high-tech industrial aquaculture. *IOP Conference Series: Earth and Environmental Science*, 403(1). <https://doi.org/10.1088/1755-1315/403/1/012220>
- Suryaningsih, W., Maulana, R., Istiqomah, I., & Isnansetyo, A. (2021). In vitro adhesion of *Bacillus* sp. And *Enterobacter* sp. probiotics on intestinal epithelial cells of red tilapia (*Oreochromis* sp.) and the application effects on the fish growth and survival rate. *IOP Conference Series: Earth and Environmental Science*, 919(1). <https://doi.org/10.1088/1755-1315/919/1/012056>
- Syanya, F. J., Litabas, J. A., Mathia, W. M., & Ntakirutimana, R. (2023). Nutritional Fish Diseases in Aquaculture: A Human Health Hazard or Mythical Theory: An Overview. *European Journal of Nutrition & Food Safety*, 15(8), 41–58. <https://doi.org/10.9734/ejnfs/2023/v15i81326>
- Syanya, F. J., Mathia, W. M., & Harikrishnan, M. (2023). Current Status and Trend on the Adoption of Fish Feed Additives for Sustainable Tilapia Aquaculture Production: A Review. *Asian Journal of Fisheries and Aquatic Research*, 22(3), 10–25. <https://doi.org/10.9734/ajfar/2023/v22i3571>
- Tabassum, T., Sofi Uddin Mahamud, A. G. M., Acharjee, T. K., Hassan, R., Akter Snigdha, T., Islam, T., Alam, R., Khoiam, M. U., Akter, F., Azad, M. R., Al Mahamud, M. A., Ahmed, G. U., & Rahman, T. (2021). Probiotic supplementations improve growth, water quality, hematology, gut microbiota and intestinal morphology of Nile tilapia. *Aquaculture Reports*, 21. <https://doi.org/10.1016/j.aqrep.2021.100972>
- Tachibana, L., Telli, G. S., de Carla Dias, D., Gonçalves, G. S., Ishikawa, C. M., Cavalcante, R. B., Natori, M. M., Hamed, S. Ben, & Ranzani-Paiva, M. J. T. (2020). Effect of feeding strategy of probiotic

- Enterococcus faecium* on growth performance, hematologic, biochemical parameters and non-specific immune response of Nile tilapia. *Aquaculture Reports*, 16.
<https://doi.org/10.1016/j.aqrep.2020.100277>
- Tachibana, L., Telli, G. S., Dias, D. de C., Gonçalves, G. S., Guimarães, M. C., Ishikawa, C. M., Cavalcante, R. B., Natori, M. M., Fernandez Alarcon, M. F., Tapia-Paniagua, S., Morifñigo, M. Á., Moyano, F. J., de Araújo, E. R. L., & Ranzani-Paiva, M. J. T. (2021). *Bacillus subtilis* and *Bacillus licheniformis* in diets for Nile tilapia (*Oreochromis niloticus*): Effects on growth performance, gut microbiota modulation and innate immunology. *Aquaculture Research*, 52(4), 1630–1642.
<https://doi.org/10.1111/are.15016>
- Talwar, C., Nagar, S., Lal, R., & Negi, R. K. (2018). Fish Gut Microbiome: Current Approaches and Future Perspectives. In *Indian Journal of Microbiology* (Vol. 58, Issue 4, pp. 397–414). Springer.
<https://doi.org/10.1007/s12088-018-0760-y>
- Tan, H. Y., Chen, S. W., & Hu, S. Y. (2019). Improvements in the growth performance, immunity, disease resistance, and gut microbiota by the probiotic *Rummeliibacillus stabekisii* in Nile tilapia (*Oreochromis niloticus*). *Fish and Shellfish Immunology*, 92, 265–275.
<https://doi.org/10.1016/j.fsi.2019.06.027>
- Thanh, N. C., Devi Rajeswari, V., Narayanan, M., Kandasamy, S., Chinnathambi, A., Ali Alharbi, S., Van Le, Q., & Kathirvel, B. (2021a). Evaluation of probiotic susceptibility of virulent *Aeromonas* sp. by a study on gut histology of *Cyprinus carpio*. *Process Biochemistry*, 111, 154–159.
<https://doi.org/10.1016/j.procbio.2021.10.023>
- Thanh, N. C., Devi Rajeswari, V., Narayanan, M., Kandasamy, S., Chinnathambi, A., Ali Alharbi, S., Van Le, Q., & Kathirvel, B. (2021b). Evaluation of probiotic susceptibility of virulent *Aeromonas* sp. by a study on gut histology of *Cyprinus carpio*. *Process Biochemistry*, 111, 154–159.
<https://doi.org/10.1016/j.procbio.2021.10.023>
- Toxqui-Rodríguez, S., Naya-Català, F., Sitjà-Bobadilla, A., Piazzon, M. C., & Pérez-Sánchez, J. (2023). Fish microbiomics: Strengths and limitations of MinION sequencing of gilthead sea bream (*Sparus aurata*) intestinal microbiota. *Aquaculture*, 569.
<https://doi.org/10.1016/j.aquaculture.2023.739388>
- Vallejo-Cordoba, B., Castro-López, C., García, H. S., González-Córdova, A. F., & Hernández-Mendoza, A. (2020). Postbiotics and paraprobiotics: A review of current evidence and emerging trends. In *Advances in Food and Nutrition Research* (Vol. 94, pp. 1–34). Academic Press Inc.
<https://doi.org/10.1016/bs.afnr.2020.06.001>
- Waiyamitra, P., Zoral, M. A., Saengtienchai, A., Luengnaruemitchai, A., Decamp, O., Gorgoglione, B., & Surachetpong, W. (2020). Probiotics modulate tilapia resistance and immune response against tilapia lake virus infection. *Pathogens*, 9(11), 1–15. <https://doi.org/10.3390/pathogens9110919>
- Wang, A. R., Ran, C., Ringø, E., & Zhou, Z. G. (2018). Progress in fish gastrointestinal microbiota research. In *Reviews in Aquaculture* (Vol. 10, Issue 3, pp. 626–640). Wiley-Blackwell.
<https://doi.org/10.1111/raq.12191>
- Wang, J., Zhang, D., Wang, Y., Liu, Z., Liu, L., & Shi, C. (2021). Probiotic effects of the *Bacillus velezensis* GY65 strain in the mandarin fish, *Siniperca chuatsi*. *Aquaculture Reports*, 21.
<https://doi.org/10.1016/j.aqrep.2021.100902>

- Wu, H. J., & Wu, E. (2012). The role of gut microbiota in immune homeostasis and autoimmunity. In *Gut Microbes* (Vol. 3, Issue 1). Landes Bioscience. <https://doi.org/10.4161/gmic.19320>
- Wu, Y., Jha, R., Li, A., Liu, H., Zhang, Z., Zhang, C., Zhai, Q., & Zhang, J. (2022). Probiotics (Lactobacillus plantarum HNU082) Supplementation Relieves Ulcerative Colitis by Affecting Intestinal Barrier Functions, Immunity-Related Gene Expression, Gut Microbiota, and Metabolic Pathways in Mice. *Microbiology Spectrum*, *10*(6). <https://doi.org/10.1128/spectrum.01651-22>
- Wuertz, S., Schroeder, A., & Wanka, K. M. (2021). Probiotics in fish nutrition—long-standing household remedy or native nutraceuticals? In *Water (Switzerland)* (Vol. 13, Issue 10). MDPI AG. <https://doi.org/10.3390/w13101348>
- Xia, Y., Lu, M., Chen, G., Cao, J., Gao, F., Wang, M., Liu, Z., Zhang, D., Zhu, H., & Yi, M. (2018). Effects of dietary Lactobacillus rhamnosus JCM1136 and Lactococcus lactis subsp. lactis JCM5805 on the growth, intestinal microbiota, morphology, immune response and disease resistance of juvenile Nile tilapia, Oreochromis niloticus. *Fish and Shellfish Immunology*, *76*, 368–379. <https://doi.org/10.1016/j.fsi.2018.03.020>
- Xia, Y., Wang, M., Gao, F., Lu, M., & Chen, G. (2020a). Effects of dietary probiotic supplementation on the growth, gut health and disease resistance of juvenile Nile tilapia (Oreochromis niloticus). *Animal Nutrition*, *6*(1), 69–79. <https://doi.org/10.1016/j.aninu.2019.07.002>
- Xia, Y., Wang, M., Gao, F., Lu, M., & Chen, G. (2020b). Effects of dietary probiotic supplementation on the growth, gut health and disease resistance of juvenile Nile tilapia (Oreochromis niloticus). *Animal Nutrition*, *6*(1), 69–79. <https://doi.org/10.1016/j.aninu.2019.07.002>
- Xia, Y., Yu, E. M., Lu, M., & Xie, J. (2020a). Effects of probiotic supplementation on gut microbiota as well as metabolite profiles within Nile tilapia, Oreochromis niloticus. *Aquaculture*, *527*. <https://doi.org/10.1016/j.aquaculture.2020.735428>
- Xia, Y., Yu, E. M., Lu, M., & Xie, J. (2020b). Effects of probiotic supplementation on gut microbiota as well as metabolite profiles within Nile tilapia, Oreochromis niloticus. *Aquaculture*, *527*. <https://doi.org/10.1016/j.aquaculture.2020.735428>
- Yadav, S., & Jha, R. (2019). Strategies to modulate the intestinal microbiota and their effects on nutrient utilization, performance, and health of poultry. In *Journal of Animal Science and Biotechnology* (Vol. 10, Issue 1). BioMed Central Ltd. <https://doi.org/10.1186/s40104-018-0310-9>
- Yang, G., Cao, H., Jiang, W., Hu, B., Jian, S., Wen, C., Kajbaf, K., Kumar, V., Tao, Z., & Peng, M. (2019). Dietary supplementation of Bacillus cereus as probiotics in Pengze crucian carp (Carassius auratus var. Pengze): Effects on growth performance, fillet quality, serum biochemical parameters and intestinal histology. *Aquaculture Research*, *50*(8), 2207–2217. <https://doi.org/10.1111/are.14102>
- Yang, G., Cui, X., Liu, S., Lu, J., Hou, X., Meng, W., Zhu, R., Zhang, W., Zhang, H., Zheng, W., & Fang, Y. (2021). Effects of dietary Lactobacillus helveticus on the growth rate, disease resistance and intestinal health of pond loach (Misgurnus anguillicaudatus). *Aquaculture*, *544*. <https://doi.org/10.1016/j.aquaculture.2021.737038>
- Yang, H. L., Liu, Z. Y., Jin, Y. M., Liu, Z. X., Zhang, B. Y., Yuan, Z. H., Ye, J. D., & Sun, Y. Z. (2022). Preventive and reparative functions of host-associated probiotics against soybean meal induced

growth, immune suppression and gut injury in Japanese seabass (*Lateolabrax japonicus*). *Fish and Shellfish Immunology*, 128, 651–663. <https://doi.org/10.1016/j.fsi.2022.08.034>

Yang, S., & Yu, M. (2021). Role of goblet cells in intestinal barrier and mucosal immunity. In *Journal of Inflammation Research* (Vol. 14, pp. 3171–3183). Dove Medical Press Ltd. <https://doi.org/10.2147/JIR.S318327>

Yukgehnaish, K., Kumar, P., Sivachandran, P., Marimuthu, K., Arshad, A., Paray, B. A., & Arockiaraj, J. (2020). Gut microbiota metagenomics in aquaculture: factors influencing gut microbiome and its physiological role in fish. In *Reviews in Aquaculture* (Vol. 12, Issue 3, pp. 1903–1927). Wiley-Blackwell. <https://doi.org/10.1111/raq.12416>

Zhang, D., Gao, Y., Ke, X., Yi, M., Liu, Z., Han, X., Shi, C., & Lu, M. (2019). *Bacillus velezensis* LF01: in vitro antimicrobial activity against fish pathogens, growth performance enhancement, and disease resistance against streptococcosis in Nile tilapia (*Oreochromis niloticus*). *Applied Microbiology and Biotechnology*, 103(21–22), 9023–9035. <https://doi.org/10.1007/s00253-019-10176-8>

Zhang, D. X., Kang, Y. H., Zhan, S., Zhao, Z. L., Jin, S. N., Chen, C., Zhang, L., Shen, J. Y., Wang, C. F., Wang, G. Q., Shan, X. F., & Qian, A. D. (2019). Effect of *Bacillus velezensis* on *Aeromonas veronii*-Induced Intestinal Mucosal Barrier Function Damage and Inflammation in Crucian Carp (*Carassius auratus*). *Frontiers in Microbiology*, 10. <https://doi.org/10.3389/fmicb.2019.02663>

Zhang, J. J., Yang, H. L., Yan, Y. Y., Zhang, C. X., Ye, J. dan, & Sun, Y. Z. (2020). Effects of fish origin probiotics on growth performance, immune response and intestinal health of shrimp (*Litopenaeus vannamei*) fed diets with fish meal partially replaced by soybean meal. *Aquaculture Nutrition*, 26(4), 1255–1265. <https://doi.org/10.1111/anu.13081>

Zhao, C., Men, X., Dang, Y., Zhou, Y., & Ren, Y. (2023). Probiotics Mediate Intestinal Microbiome and Microbiota-Derived Metabolites Regulating the Growth and Immunity of Rainbow Trout (*Oncorhynchus mykiss*). *Microbiology Spectrum*, 11(2). <https://doi.org/10.1128/spectrum.03980-22>

Zhaxi, Y., Meng, X., Wang, W., Wang, L., He, Z., Zhang, X., & Pu, W. (2020). Duan-Nai-An, A Yeast Probiotic, Improves Intestinal Mucosa Integrity and Immune Function in Weaned Piglets. *Scientific Reports*, 10(1). <https://doi.org/10.1038/s41598-020-61279-6>

Zheng, D., Liwinski, T., & Elinav, E. (2020). Interaction between microbiota and immunity in health and disease. In *Cell Research* (Vol. 30, Issue 6, pp. 492–506). Springer Nature. <https://doi.org/10.1038/s41422-020-0332-7>