Annual Methodological Archive Research Review
http://amresearchreview.com/index.php/Journal/about
Volume 3, Issue 10 (2025)

Online ISSN 3007-3197
Print ISSN 3007-3189

http://amresearchreview.com/index.php/Journal/about

THE ROLE OF FEED SUPPLEMENTATION ON GUT MICROBIOTA IN CULTURABLE CARPS: A COMPREHENSIVE REVIEW

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ABSTRACT

Carps are among the most valuable freshwater fish worldwide, with their intestinal microbiota playing a vital role in regulating nutrient assimilation, immune defense, and resistance to pathogens. In recent years, dietary interventions have gained considerable attention as a means to manipulate gut microbial communities and improve the overall health and productivity of cultured carp species. This review provides an in-depth analysis of the influence of different dietary supplements such as probiotics, prebiotics, synbiotics, polysaccharides, carotenoids, plant extracts, and

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microbial cultures on gut microbiota composition, growth efficiency, antioxidant capacity, and immune responses in key carp species, including Cyprinus carpio (common carp), Hypophthalmichthys molitrix (silver carp), Hypophthalmichthys nobilis (bighead carp), Carassius auratus (crucian carp), Mylopharyngodon piceus (black carp), and koi carp. Most findings demonstrate that these dietary additives foster the proliferation of beneficial bacterial groups such as Lactobacillus, Bifidobacterium, and Cetobacterium, while inhibiting pathogenic microorganisms and enhancing metabolic processes related to carbohydrate and amino acid utilization. Furthermore, bioactive compounds like polysaccharides and probiotics have been consistently shown to strengthen antioxidant defense mechanisms and upregulate immune-related gene expression, contributing to improved growth performance and resilience against stress. Nonetheless, the effectiveness of these supplements can vary depending on factors such as dosage, feeding duration, and environmental conditions. A deeper understanding of the interactions between gut microbes and dietary components is essential for developing sustainable aquaculture strategies and optimized nutritional management practices in carp farming systems.

Keywords: Carp, Dietary Supplementation, Gut Microbiota, Probiotics, Aquaculture Nutrition, Immune Response, Growth Performance

INTRODUCTION

Back ground on aquaculture and culturable carps

Aquaculture has experienced continuous global growth and is increasingly recognized as a key solution to meeting the rising demand for aquatic food products. It serves as a sustainable alternative for enhancing fisheries resources and restoring aquatic ecosystems.(Subasinghe et al., 2009)(Subasinghe, 2017). Aquaculture holds a vital position in the global food economy, providing an essential source of nutrition and income for millions worldwide. It is estimated that nearly 200 million individuals rely directly on fisheries and marine resources for their employment and livelihoods. (Pradeepkiran et al., 2019). Aquaculture has shown consistent expansion across nearly all regions of the world, with the majority of this growth occurring in Asia particularly in China. Global aquaculture output has increased significantly, rising from about 7.8 million tonnes in 1980 to around 114.5 million tonnes in 2018 (Bartley et al., 2022). Excluding aquatic plants, aquaculture production has shown notable advancement, increasing from about 4.7 million tonnes in 1980 to nearly 82.1 million tonnes in 2018 (FAO 2020;Ahmed et al., 2020).

The production from capture fisheries has reached a plateau, as most major fishing grounds are already exploited to their maximum sustainable potential. Consequently, capture fisheries alone are insufficient to satisfy the escalating global demand for aquatic food resources. In this regard, aquaculture represents a viable and sustainable approach to bridging the widening gap between the supply and demand of aquatic products in various regions worldwide.

The accelerating growth of the global population has exacerbated food insecurity, with an estimated 821 million people currently suffering from hunger. Additionally, around 14% of the global population faces deficiencies in protein and energy intake, reflecting the widening disparity between food production capacity and nutritional

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Volume 3, Issue 10 (2025)

Online ISSN 3007-3197
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requirements. Tackling these challenges is vital for ensuring global food security, particularly as traditional food production systems are progressively unable to satisfy the demands of an expanding population. In 2020, developing countries contributed nearly 79% of the total global fish production, emphasizing their crucial role in advancing the aquaculture and fisheries sectors worldwide.(Squires & Gaur, 2020).

Globally, over 29,000 fish species have been documented, among which approximately 1,500 hold established commercial significance. The aquaculture industry continues to exhibit steady growth, largely driven by innovations in sustainable production systems. Notably, biofloc technology has emerged as an efficient and eco-friendly alternative to conventional aquaculture methods, enhancing resource utilization and offering distinct advantages in areas constrained by limited land availability. Commonly cultured species include Tilapia spp., Clarias gariepinus, and Cyprinus carpio. (Gul et al., 2024).

Many regions and nations have recognized aquaculture as one of the most sustainable approaches for enhancing fish production and promoting economic growth (FAO, 2021f). According to United Nations projections, population expansion in sub-Saharan Africa is expected to contribute more than half of the global population increase between 2019 and 2050 (UN, 2019a), while populations in many parts of Asia, Latin America and the Caribbean, Europe and North America are projected to peak and to begin to decline before the end of this century. According to the UN (2019a), "the 47 least developed countries are among the world's fastest growing – many are projected to double in population between 2019 and 2050 – putting pressure on already strained resources". The increased population as well as economic and regional differences will present both opportunities and challenges for aquaculture.(Bartley et al., 2022).

The gut microbiota serves as a critical interface between diet, host physiology, and the aquatic environment (Xiong et al., 2019). It influences nutrient metabolism, pathogen resistance, and immune modulation. In carps, the gut microbial ecosystem is dynamic and influenced by multiple factors including diet composition, rearing environment, and fish developmental stage (Zhou et al., 2022). Disruptions in microbial balance can lead to dysbiosis, negatively impacting growth and health. Therefore, understanding the role of feed supplementation in shaping gut microbial communities is fundamental for improving aquaculture productivity and sustainability.

Feed supplements such as probiotics, prebiotics, synbiotics, phytogenic compounds, enzymes, and organic acids have shown promising effects in maintaining gut homeostasis and enhancing fish performance (Abdelhamid et al., 2023). These supplements influence intestinal microbial populations by enhancing beneficial bacteria such as Lactobacillus, Bacillus, and Aeromonas species while suppressing pathogenic taxa. Moreover, modern molecular techniques, including next-generation sequencing (NGS) and metagenomic profiling, have provided deep insights into microbial diversity and functional pathways (Ghosh et al., 2022).

The review aims to consolidate the available evidence from recent studies (2015–2025) focusing on how different feed additives affect gut microbial composition and function in culturable carps. It also discusses mechanisms of action, health implications, and research directions for future feed innovations.

Carp, belonging to the family **Cyprinidae,** originated in China and have successfully

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expanded across Asia and Europe over time. Today, they are recognized as one of the most important aquaculture species worldwide, with production anticipated to rise in response to increasing global market demand. (Goh et al., 2023). This family is the largest family of fish and includes 220 genera and 2420 species (Forouhar Vajargah et al., 2018). Most species in this family inhabit freshwater environments, and even those that tolerate brackish water must return to freshwater to reproduce. Among them, the common carp stands out as one of the most significant members. It is regarded as one of the most widely distributed and extensively bred freshwater fish species across the world (Vajargah & Vatandoust, 2022).Carp species are among the most widely cultured freshwater fishes globally due to their robustness and economic importance. Optimizing feed strategies in carp aquaculture is crucial to enhance production efficiency while reducing disease and environmental impacts. The fish gut microbiota is increasingly recognized as a key determinant of host health and performance; thus, targeted feed supplementation is an attractive strategy to steer the microbiome toward beneficial configurations the microbiota can influence digestion, immune responses, and energy homeostasis in fish. (Butt & Volkoff, 2019)

Common carp

The common carp (Cyprinus carpio), a member of the order **Cypriniformes** and the family **Cyprinidae** the largest group of freshwater fishes primarily lives in freshwater habitats such as ponds, lakes, and rivers, though it can occasionally be found in slightly brackish waters. Globally, it ranks as the third most extensively farmed and economically significant freshwater fish species.(Rahman, 2015). The common carp is the second most significant species in European freshwater aquaculture, with a production volume of about 164,755 tons recorded in 2017 (FAO, 2019). While it is occasionally found in slightly brackish habitats, it predominantly thrives in freshwater environments such as ponds, lakes, and rivers. Being an omnivorous species, the common carp (Cyprinus carpio L.) also contributes positively to ecological balance and environmental sustainability.(Colombo et al., 2023)

Grass carp

Grass carp are naturally distributed in most rivers in China, except for the northwest region. They are also found from the Heilungkiang (Amur River) basin in eastern Asia to Thailand and Vietnam. But the area inhabited by grass carp has been greatly expanded in recent years. They have been introduced into the freshwaters of many regions in the world, such as central Asia, Japan, America, Europe, and the Arabian peninsula. (Saha et al., 2006) Grass carp is a very popular cultured fish, mainly because of its ability to feed on various plants. In addition, it grows rapidly to large sizes and has good meat quality. In pond culture, it can be polycultured with other fish (Bartley, 2022)

Crusian carp

Crucian carp (Carassius auratus), a member of the Cyprinidae family, is among the most significant freshwater aquaculture species in China. Its popularity among consumers and fish farmers stems from its tasty and nutritious flesh, rapid growth, strong disease resistance, and other desirable traits. (Ding et al., 2023). Crucian carp,

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a widespread cyprinid fish native to Eurasia, exhibits remarkable contrasts in its physiology and ecology at both individual and population scales. These differences are closely linked to the specific communities and ecosystems they inhabit, particularly when comparing populations found in monoculture environments. Historically, two distinct forms of crucian carp have been identified, though their classification has varied over time. Owing to its unique traits, the crucian carp serves as an excellent model organism for studying ecological interactions such as competition and predation. Moreover, its strong tolerance to harsh environmental conditions highlights its potential value in aquaculture, especially for developing hybrids with greater survival abilities than the common carp. (Holopainen et al., 1997)

Carps	Dietary supplements	Effects	reference
common carp	Carotenoids **Fermentable oligosaccharides** **Synbiotics** Anthocyanin	• Growth Performance • Increased microbial diversity • Increase Body weight	(Feher et al., 2021)
	Bacterial Culture of Fengycin-Producing Bacillus subtilis (B. subtilis)	• Growth Performance • Good Immune response • Increased expression of gut physical barrier-related genes • Increased abundance of Fusobacteriota and Cetobacterium • Disease Resistance	(Xia et al., 2024)
	Carbohydrate-Based Diets	• Negative impact on intestinal health • Gut Microbiota Alterations	(Xiong et al., 2024)
	Humulus scandens Extract (a plant-derived supplement)	• improved **growth performance** • **antioxidant enzyme activity, and intestinal health**	(bin Li et al., 2023)
Koi carp/ common carp	Herba Houttuyniae (H. houttuyniae) Extract	• improved **intestinal structure** • **digestive enzyme activity** • **beneficial gut microbiota**	(Qiu et al., 2024)

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	Biofloc Meal (BM) as a replacement for Fish Meal (FM)	• improved **growth** • **Digestion protein, lipid metabolism and immunity** • **antioxidant capacity**	(Wei et al., 2024)
	Solid-state fermentation product of Bacillus velezensis T23	• improved **growth, liver and gut health,** • **antioxidant capacity and immune response**	(X. Chen et al., 2025)
	Lactic Acid (LA)	• improved growth performance • feed efficiency, and intestinal enzyme activity	(Hoseini et al., 2023)
	Lactobacillus rhamnosus fermentation product (GCC-3)	• improved liver health • enhanced gut microbiota	(J. Chen et al., 2024)
	Solid-state fermentation product of yeast (SFPY)	• improved **liver and intestinal health** • enhancing gut microbiota composition • enhanced **disease resistance**	(Wang et al., 2024)
	Dietary supplementation with **TB** (Tributyrin)	• improved **intestinal function, morphology, and microbiota balance** • **higher growth performance and feed efficiency**	(D. Xie et al., 2021)
	Stabilized Fermentation Product of Cetobacterium somerae (XMX-1)	• improved **gut health** • **liver function** • **antioxidant capacity**	(M. Xie et al., 2022)
Grass Carp	1.(Dietary Protein Sources) Plant Protein-Based Diet Fishmeal-Based Diet **2.Extrusion Temperature (ET)**	• Improved growth performance Positively influenced gut microbiota	(Z. Zhang, Yang, et al., 2025)
	Clostridium autoethanogenum Protein (CAP)	• Positive Effect on Growth • enhancing the fish's immune ability	(G. Liu et al., 2024)

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	• Improved Intestinal Structure	
(Probiotics)Bacillus spp. Lactobacillus spp. Enterococcus faecium, Saccharomyces cerevisiae (Prebiotics) Inulin, Fructooligosaccharides (FOS)	• enhance the growth of beneficial bacteria • reduce pathogenic bacteria • improve gut diversity • enhanced immune defenses	(Y. Zhang et al., 2023)
Sanguinarine (SG) Cottonseed and Rapeseed Meal	• improved survival rate • Enhanced Immunity • beneficial for improving **intestinal integrity** • **microbial balance**	(Y.-L. Liu et al., 2020)
duo-strain probiotics with post-spraying technology	• improved the growth performance • Positive Changes in Gut Health • reduced oxidative stress	(Luo et al., 2022)
Probiotics PrebiotIcs Synbiotics	• Enhances gut microbial diversity improves digestion, and boosts immunity	(Tran et al., 2017)
Sanguinarine Supplementation	• improved the intestinal immune function and physical barrier • overall intestinal health • immune function, and microbiota stability	(Shi et al., 2023)
Vitamins & Minerals Probiotics & Prebiotics Fatty Acid Supplements Antioxidants Enzymes	• reducing oxidative stress and improving immune responses • promote gut health by regulating intestinal microbiota • improving digestion • enhancing disease resistance	(G. Liu et al., 2022)
Sanguinarine Cottonseed Protein	• enhance growth boost immunity	(Z. Zhang, Chen, et al.,

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	Concentrate Probiotics (e.g., Lactobacillus, Bacillus, Pediococcus) **Prebiotics (e.g., Fructooligosaccharides, Mannan-oligosaccharides)**	• improve gut health • strengthen antioxidant defenses • regulate metabolism	2025)
Silver Carp	Probiotic + Prebiotic (Pediococcus acidilactici + Agaricus bisporus)	• Improved mucus indices; enhanced gut barrier / mucosal immunity	(Houshmand et al., 2022)
	Herbal feed supplement: Turmeric (TU) + Ginger (GN)	• Recuperative effects under heavy metals toxicity • improved physiology and histopathology • Improved immune and gut integrity	(Maqaddas et al., 2025)
	Alginic acid + Glycyrrhizic acid	• Improved growth performance • better feed utilization; immune modulation	(Harikrishnan et al., 2022)
	Dietary organic selenium, vitamin C, and vitamin E	• Improved growth performance • better serum biochemistry • Improved antioxidant status	(Yu et al., 2025)
	Micro- and nano-scale chitosan	• Improved growth performance • improved non-specific immunity • Resistance to Staphylococcus aureus	(Younus et al., 2020)
Koi carp	Bacillus subtilis C-3102 (probiotic)	• Growth Performance changes in predominant intestinal microbiota	(He et al., 2011)
	Plant polyphenols (Curcumin, Resveratrol, Chlorogenic Acid, etc.)	• Altered gut microbial structure • SCFA; antioxidant enzymes (SOD, lysozyme), blood glucose & insulin	(Zhang et al., 2022)

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	Trans-Galactooligosaccharide (prebiotic)	• Positive effects on intestine morphometry, likely improved gut health	(Ziółkowska et al., 2020)
	Bacillus subtilis HGCC-1	• Improved growth performance • modulation of gut microbiota • enhanced host health indicators	(Li et al., 2025)
Gold Fish	Lactobacillus helveticus CD6 probiotic	• Improved antioxidant levels, better absorption of essential trace elements (Fe, Zn) • reduced mortalities • slight improvements in weight gain vs control	(Ramasamy et al., 2018)
	Prebiotics: GroBiotic-A, MOS, GOS, FOS (1%) with fish meal / soybean meal diet	• No effect on apparent digestibility • no marked changes in GI microbiota diversity (DGGE)	(Raggi et al., 2012)
	Dairy-yeast prebiotic (GroBiotic-A, 2%) under different culture systems (with/without phytoplankton & zooplankton)	• Some improvement in weight gain and feed efficiency when phytoplankton/zooplankton present; but prebiotic did not significantly enhance resistance to Aeromonas hydrophila • little change in microbiota by DGGE	(Raggi et al., 2008)
	Alteration of feed type: pellet vs live food vs alternating feeds	• Changes in gut microbial community: shift from Proteobacteria to Firmicutes • increases in Bacteroidetes etc. • diversity increased with alternating feeds • water/intestine microbiomes	(Wang et al., 2023)

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		influenced by feed type	
	Bacillus cereus probiotic	• Increased survival, weight gain, improved FCR & SGR • reduced mortality	(Preprint, 2023)
	Probiotics in diet (various effective microorganisms EM-4)	• Improved growth and survival; best dose around 30 ml/kg feed	(Hasan et al., 2018)
Crucian carp	**Ginger polysaccharide (GP)** at 0.1-0.2-0.4-0.8 %	• Growth performance (best at 0.4 %); digestive enzyme activity • antioxidant capacity • serum lysozyme • immune gene expression (TNF-α, IL-8, IFN-γ, NF-κB), IL-10 and TGF-β; changes in gut microbiota (Fusobacteriota & Firmicutes); improved disease resistance to Aeromonas hydrophila	(Fei et al., 2023)
	Lactic acid bacteria (Lactococcus lactis strains	• Lower mortality vs control; changed gut microbiota Firmicutes Proteobacteria • Actinobacteria); immune responses modulated under temperature stress	(Liu et al., 2022)
	Tea Polyphenols (TPs) (200 mg/kg optimal) under chronic crowding stress	• Improved growth; enhanced antioxidant enzyme activities • restored gut microbiota by reducing Proteobacteria and increasing Firmicutes • decreased abundance of stress-associated pathogens	(Zhang et al., 2023)
	Hawthorn Polysaccharide (HP)	• Improved immunity and antioxidant	(Liu et al., 2023)

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challenged with Aeromonas hydrophila	performance • enhanced intestinal microbiota structure • improved metabolic level; better resistance to pathogen challenge

The role of gut microbiota in fish health and performance

Fish are poikilothermic (cold-blooded) aquatic organisms that include a wide diversity of species, ranging from vertebrates to invertebrates within the animal kingdom. They serve as an excellent source of lean, high-quality protein and are rich in omega-3 fatty acids, essential vitamins such as B2 and D, and important minerals including iron, calcium, phosphorus, iodine, magnesium, zinc, and potassium.(Austin, 2002). The gut microbiota comprises a diverse community of microorganisms residing in the gastrointestinal tract that play a crucial role in the host's health by contributing to digestion, metabolism, and waste elimination. The main phyla of gut microbiota are Bacteroidetes, firmicutes, fusobacteria, proteobacteria, cyanobacteria, verrucomicr obia, and Actinobacteria.

Gut Microbiota in Culturable Carps

The intestinal microbiota of carps is complex and species-specific, influenced by environmental, nutritional, and physiological factors (Wu et al., 2020). Common bacterial phyla include Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria, each contributing differently to digestion and immune responses (Roeselers et al., 2017). In Cyprinus carpio, Firmicutes and Proteobacteria dominate, reflecting a balance between carbohydrate fermenters and opportunistic bacteria (Bakke-McKellep et al., 2022).

Feed quality directly affects microbial richness and diversity. Diets with higher plant ingredients or non-digestible polysaccharides can alter microbial fermentation patterns and increase short-chain fatty acid (SCFA) production, which supports intestinal epithelial integrity (Zhang et al., 2023). In contrast, high-protein or lipid-rich diets may lead to microbial imbalance, reducing beneficial taxa and promoting potential pathogens (Liu et al., 2018).

The role of the gut microbiota extends beyond digestion it modulates immune signaling, oxidative stress, and disease resistance (Liang et al., 2020). For instance, supplementation with Bacillus subtilis has been reported to enhance Labeo rohita's immune gene expression (IL-1β, TNF-α) and improve feed conversion ratio (Kumar et al., 2021). Similarly, prebiotics such as inulin and mannan oligosaccharides (MOS) foster beneficial microbial populations and improve growth performance in Cirrhinus mrigala (Das et al., 2019).

Overall, maintaining a balanced gut microbiota through targeted feed supplementation can significantly enhance health resilience and nutrient utilization in carps.

Composition and diversity of gut microbiota in carps

Factors influencing microbiota composition: genetics, environment, diet, and rearing conditions.

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Key roles of gut microbiota:
Nutrient metabolism
Immune system modulation
Disease resistance
Feed Supplementation Categories and Mechanisms

Probiotics

Probiotics are live microorganisms that confer health benefits when administered in adequate amounts, primarily by enhancing gut microbial balance and immune competence (Merrifield et al., 2018). In aquaculture, probiotic supplementation is one of the most widely studied approaches to modulate intestinal microbiota and improve fish performance. Strains belonging to Bacillus, Lactobacillus, Enterococcus, and Pediococcus are frequently used due to their resilience and enzyme-producing capabilities (Ghosh et al., 2022).

In Labeo rohita, dietary Bacillus subtilis supplementation increased the relative abundance of beneficial Firmicutes while suppressing opportunistic Aeromonas species, thereby improving feed conversion ratio (FCR) and immune gene expression (Kumar et al., 2021). Similarly, Lactobacillus plantarum improved intestinal villi morphology, lysozyme activity, and disease resistance against Aeromonas hydrophila in Cyprinus carpio (Abdelhamid et al., 2023). The primary mechanisms involve competitive exclusion of pathogens, production of antimicrobial peptides, and enhancement of mucosal immunity through cytokine regulation (Hai, 2015).

Metagenomic analyses have revealed that probiotics also promote carbohydrate metabolism and short-chain fatty acid (SCFA) synthesis, particularly butyrate, which is critical for gut epithelial integrity (Zhou et al., 2023). However, probiotic efficacy depends on strain selection, dosage, and environmental factors such as temperature and water quality (Nguyen et al., 2019). Combining probiotics with prebiotics or herbal additives has emerged as a synergistic strategy, forming the basis for synbiotic applications discussed below.

Prebiotics

Prebiotics are non-digestible food components that selectively stimulate the growth and activity of beneficial microbes in the intestine (Gibson et al., 2017). Common prebiotics in carp diets include mannan oligosaccharides (MOS), inulin, fructooligosaccharides (FOS), and β-glucans. In Cirrhinus mrigala, dietary MOS increased microbial diversity, improved digestive enzyme activity, and enhanced growth rate (Das et al., 2019).

Mechanistically, prebiotics act as fermentable substrates for beneficial bacteria, promoting SCFA production and lowering intestinal pH, which suppresses pathogenic growth (Ringø et al., 2020). They also enhance mucosal barrier function and modulate innate immune markers such as lysozyme and complement activity (Liang et al., 2020). In Labeo rohita, inulin supplementation improved hematological indices and reduced oxidative stress under high-density conditions (Zhang et al., 2021).

Recent molecular studies have confirmed that prebiotic feeding alters core microbiota composition, increasing Lactobacillus and Bifidobacterium populations while reducing Pseudomonas and Aeromonas (Wu et al., 2020). These microbial shifts

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correspond to improved nutrient absorption and disease resilience, highlighting prebiotics as valuable functional feed ingredients.

Synbiotics

Synbiotics combine probiotics and prebiotics, providing both beneficial microbes and substrates that support their colonization and function. The synergistic interaction enhances microbial stability and resilience to environmental fluctuations (Kumar et al., 2022). In Catla catla, a synbiotic mixture of Bacillus subtilis and MOS improved weight gain, FCR, and immune gene expression more effectively than either component alone (Singh et al., 2020).

The mechanisms underlying synbiotic benefits include enhanced colonization of probiotics in the gut, elevated SCFA production, and improved nutrient digestibility (Zhou et al., 2023). Synbiotics also regulate the expression of intestinal tight-junction proteins, thereby maintaining barrier integrity and preventing pathogen translocation (Li et al., 2021). Future research is exploring tailored synbiotic formulations based on carp species and life stage to maximize microbial and physiological outcomes.

Phytogenic Feed Additives

Phytogenic additives (plant-derived bioactives such as essential oils, polyphenols, and flavonoids) have gained attention for their antioxidant, antimicrobial, and immune-boosting properties (Reverter et al., 2017). In Cyprinus carpio, supplementation with garlic (Allium sativum) extract improved gut microbial balance, increased Lactobacillus populations, and reduced intestinal Vibrio counts (Jahan et al., 2019).

Similarly, dietary inclusion of turmeric (Curcuma longa) or oregano oil has been shown to enhance intestinal antioxidant enzyme activity and microbial richness (Al-Dohail et al., 2020). The active compounds in phytogenics such as allicin, curcumin, and carvacrol can disrupt bacterial cell membranes, inhibit quorum sensing, and promote beneficial microbial growth (Abdelhamid et al., 2023). However, dosage optimization is crucial, as excessive use may exert antimicrobial pressure on commensal flora or affect palatability.

Enzymes

Exogenous enzymes, including proteases, amylases, cellulases, and phytases, are used to improve feed digestibility and nutrient utilization (Liang et al., 2020). Enzyme supplementation indirectly influences gut microbiota by altering substrate availability in the intestine. In Labeo rohita, dietary protease and xylanase increased bacterial diversity and improved nitrogen retention efficiency (Bakke-McKellep et al., 2022).

Phytase supplementation has been shown to enhance phosphorus availability while reducing undigested plant material that can harbor opportunistic pathogens (Nguyen et al., 2019). Moreover, enzyme-supplemented diets often correlate with increased abundance of saccharolytic bacteria, contributing to SCFA production and improved gut health (Wu et al., 2020).

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Organic Acids and Salts

Organic acids such as citric, lactic, and formic acid are increasingly used in carp diets to stabilize gut microbiota and improve nutrient digestibility (Ringø et al., 2020). They act primarily by lowering gut pH and inhibiting pathogenic bacteria like Vibrio and Aeromonas (Liang et al., 2020). In Cyprinus carpio, sodium butyrate supplementation improved villus height, intestinal barrier function, and microbial diversity (Zhang et al., 2023).

Butyrate, a major SCFA, also acts as an energy source for enterocytes and modulates the expression of inflammatory cytokines (IL-10, TNF-α), leading to improved immune homeostasis (Li et al., 2021). A combination of organic acids with probiotics has shown additive effects, indicating a promising area for integrated feed strategies (Merrifield et al., 2018).

Mechanistic Insights into Feed Supplementation and Gut Microbiota Modulation

Nutritional-Microbial Interactions

Feed supplements alter the nutrient composition and biochemical environment of the intestine, influencing microbial metabolism and host physiology (Ringø et al., 2020). The gut ecosystem in carps serves as a dynamic site for carbohydrate fermentation, protein hydrolysis, and lipid metabolism. Probiotics and prebiotics modulate the microbiota by promoting fermentative species capable of producing short-chain fatty acids (SCFAs) such as acetate, propionate, and butyrate (Zhang et al., 2023). These SCFAs serve as signaling molecules that enhance epithelial cell proliferation, reduce oxidative stress, and modulate immune gene expression (Li et al., 2021).

The increased availability of fermentable substrates through enzyme and prebiotic supplementation stimulates the growth of saccharolytic bacteria, while reducing proteolytic fermentation that may lead to toxic metabolites such as ammonia and amines (Liu et al., 2018). Thus, an optimal feed formulation should balance macronutrient digestibility with microbial metabolic potential to prevent dysbiosis.

Immunomodulation and Disease Resistance

The gut-associated lymphoid tissue (GALT) plays a crucial role in fish immune defense. Feed supplements enhance the crosstalk between intestinal microbes and immune signaling pathways, leading to upregulation of cytokines such as interleukin-1β (IL-1β), tumor necrosis factor-alpha (TNF-α), and transforming growth factor-beta (TGF-β) (Kumar et al., 2021).

Probiotic supplementation, particularly with Bacillus subtilis and Lactobacillus plantarum, has been reported to stimulate the innate immune response and improve survival rates following bacterial challenge (Abdelhamid et al., 2023). Prebiotics and organic acids further contribute by enhancing mucin secretion and reinforcing the intestinal epithelial barrier, preventing the colonization of pathogens like Aeromonas hydrophila and Edwardsiella tarda (Zhou et al., 2023).

Furthermore, phytogenic compounds exhibit antimicrobial and anti-inflammatory effects, helping maintain immune homeostasis without antibiotic residues (Reverter et al., 2017). The synergistic combination of these additives supports disease resilience and overall performance in intensive aquaculture systems.

Annual Methodological Archive Research Review
http://amresearchreview.com/index.php/Journal/about
Volume 3, Issue 10 (2025)

Online ISSN 3007-3197
Print ISSN 3007-3189

http://amresearchreview.com/index.php/Journal/about

Oxidative Stress and Antioxidant Regulation

Feed additives also influence redox homeostasis within intestinal tissues. Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPx) are upregulated in response to phytogenic and probiotic supplementation (Jahan et al., 2019). Oxidative stress markers, including malondialdehyde (MDA), are significantly reduced when carps are fed diets enriched with turmeric, garlic extract, or synbiotics (Li et al., 2021).

These biochemical modulations not only improve gut morphology but also protect intestinal integrity during stressful farming conditions such as high density or poor water quality. This antioxidant response contributes to maintaining a stable microbial community structure that supports nutrient absorption and immunity.

Environmental and Host Factors

Environmental conditions such as temperature, dissolved oxygen, and water quality can influence both the host and its intestinal microbiota (Xiong et al., 2019). Seasonal fluctuations affect microbial community composition, while water-borne microorganisms contribute to microbial colonization in the gut (Ghosh et al., 2022). The host genotype and developmental stage also play key roles, with larval and juvenile carps showing higher microbial variability than adults.

Understanding these interactions is crucial for optimizing feed supplementation protocols. For instance, probiotics may perform differently under varying salinity or pH levels; thus, environmental standardization and microbial adaptability should be considered during feed formulation.

Knowledge Gaps and Future Research Directions

Despite significant progress in understanding the relationship between feed supplementation and gut microbiota in carps, several critical gaps remain.

Species-Specific Responses

Current research often generalizes findings across carp species, but microbiota responses vary significantly among Labeo rohita, Catla catla, and Cirrhinus mrigala. Species-specific nutritional physiology must be investigated using controlled multi-factorial studies (Li et al., 2021).

Molecular Functional Analysis

While 16S rRNA sequencing provides valuable taxonomic data, it does not reveal metabolic functions. Future studies should incorporate metatranscriptomics and metabolomics to unravel the functional roles of microbial taxa in nutrient assimilation and immune modulation (Ghosh et al., 2022).

Long-Term and Field-Level Validation

Most studies are short-term laboratory trials. There is a need for large-scale, long-duration experiments in commercial ponds to validate the stability and practicality of feed supplementation effects (Abdelhamid et al., 2023).

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http://amresearchreview.com/index.php/Journal/about

Synbiotic Optimization and Formulation

The combination ratios of probiotics and prebiotics for specific carp species remain underexplored. Novel formulations integrating multi-strain probiotics with plant-based substrates could enhance microbial colonization and resilience under stress.

Environmental Sustainability:

Feed additives should be assessed for ecological impact, including their influence on water microbiota and nutrient cycling. Sustainable feed development must align with environmental management strategies to ensure responsible aquaculture expansion (FAO, 2024).

Conclusion

Feed supplementation plays a pivotal role in maintaining intestinal health and promoting sustainable productivity in culturable carps. Probiotics, prebiotics, synbiotics, phytogenics, enzymes, and organic acids each contribute uniquely to shaping gut microbiota and enhancing immune and digestive functions. The integration of molecular microbiology with nutrition science offers new opportunities for developing targeted feed strategies that optimize gut ecology and fish welfare.

Future research should focus on species-specific responses, long-term ecological validation, and the discovery of novel microbial strains and bioactive compounds that could serve as next-generation feed additives. Strengthening the understanding of host–microbe interactions will ultimately lead to improved fish performance, disease resilience, and environmentally sustainable aquaculture practices.

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