

Review

Natural Biotics as Biocontrol Agents for Sustainable Aquaculture

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Featured Application

Probiotics, prebiotics and phytobiotics can be applied as aquafeed additives to improve animal health and minimize environmental and antimicrobial resistance risks in aquaculture.

Abstract

Aquaculture has evolved as one of the most dynamic industries in food production, representing the fastest-growing activity in meeting global food demand. Nevertheless, its rapid expansion is accompanied by significant challenges, including water pollution and the proliferation of pathogens that induce stress in aquatic organisms, leading to disease outbreaks and high mortality rates. To mitigate these problems, antibiotics and chemical agents are widely used to control infections. However, their excessive application results in residual contamination and promotes the emergence of drug-resistant bacterial strains. As a sustainable and environmentally friendly alternative, probiotics, prebiotics, and phytobiotics have attracted growing interest as substitutes for conventional chemotherapy in aquaculture. These functional feed additives enhance disease resistance and exhibit diverse bioactivities, such as antibacterial, antiviral, antifungal, and antiparasitic effects. Additionally, they improve growth performance, strengthen immune responses in cultured species, and contribute to better water quality. This review synthesizes current findings on the role of probiotics, prebiotics and phytobiotics in advancing sustainable aquaculture practices worldwide, while critically discussing their limitations, such as species-specificity, dose and duration responses, and potential long-term risks, thereby providing valuable insights to guide future research and innovation toward environmentally responsible and health-promoting solutions in the aquaculture industry.

Keywords: aquaculture; seafood; functional feed additives; sustainability; disease management



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1. Introduction

Aquaculture is widely recognized as the “blue revolution” [1] and represents the fastest-growing and most promising sector meeting global food demands [2]. For the first time in recorded history, aquaculture surpassed wild-caught fishery to become the primary source for human aquatic animals’ consumption in 2022, reaching a production of 130.9 million tons [3]. Global seafood consumption has increased significantly, driven by growing recognition of its nutritional value and its beneficial role in promoting human health [4]. Aquatic foods are a rich source of high-quality proteins, vital amino acids,

vitamins (A, B-complex, and D), and essential minerals such as phosphorus, zinc, calcium, sodium, iodine, potassium, iron, magnesium, and selenium as well as polyunsaturated fatty acids, particularly omega-3 fatty acids including eicosapentaenoic acid (EPA) and docosahexaenoic acid (DEA) [4]. Given the projected increase in the world's population to 9.7 billion by 2050, aquaculture production is expected to reach 93.6 million tons by 2030 and 140 million tons by 2050 to satisfy the future demand for seafood [5]. Consequently, the sector has intensified through the adoption of advanced husbandry practices and the development of innovative technologies [6].

However, intensive aquaculture practices increase stress in aquatic species, making them more vulnerable to bacterial, viral, fungal, and/or parasitic infections [6,7]. On top of that, environmental changes [5] and the use of chemicals for growth enhancement, including antibiotics, hormones, and pesticides, are the major constraints that may hamper the development of the aquaculture industry [2,8]. Various classes of antibiotics, such as members of the aminoglycoside, quinolone, sulfonamide, tetracycline, macrolide, chloramphenicol, β -lactam, nitrofurantoin, lincosamide, and polymyxin classes, are widely used in aquaculture [9]. These compounds are considered one of the most significant groups of emerging contaminants in aquatic ecosystems, posing serious environmental concerns due to their widespread occurrence across different environmental compartments and their potential to promote antimicrobial resistance. This includes the proliferation of antibiotic resistance in bacteria and their associated genes, which may ultimately enter the human food chain, resulting in adverse toxicological effects and long-term persistence in the environment [6,9–11]. Additionally, the application of antibiotics in aquaculture can impair the activity of beneficial gut microbiota, leading to alterations in microbial communities and disruptions in nutrient metabolism, physiological functions, and the immune competence of fish, thus enhancing their susceptibility to opportunistic pathogen infections [6].

To overcome these challenges and to minimize disease outbreaks in aquaculture practices, the utilization of biocontrol approaches such as probiotics, prebiotics and phytobiotics can be environmentally and consumer-friendly alternatives. Biocontrol strategies act as natural agents to suppress pathogens while enhancing host health. They act directly by eliminating pathogens through the synthesis of antimicrobial compounds, and through competitive exclusion of pathogens, or indirectly by enhancing host health and environmental conditions [8,12,13]. The concept of “probiotics” originates from the Greek words “pro,” indicating “for,” and “bios,” expressing “life,” demonstrating their involvement in promoting life. Thus, probiotics are beneficial microorganisms that support the host's health. While prebiotics are not classified as biocontrol agents themselves, they are compounds that are selectively used by health-promoting microorganisms to indirectly contribute to pathogen inhibition and disease control, thereby conferring benefits to the host [14]. Phytobiotics, on the other hand, encompass whole plants, specific parts of a plant, extracts, derivatives, or plant-derived bioactive substances that can be integrated into aquafeeds to improve the overall health and performance of aquatic species [15–17]. Probiotics, prebiotics and phytobiotics act as biocontrol agents to reduce pathogens and improve host health, not only by promoting feed digestibility and growth of aquaculture species but also by enhancing their immune response, thus reducing susceptibility to disease. Recently, numerous investigations have reported that the integration of probiotics, prebiotics, and phytobiotics can provide significant benefits to aquaculture, demonstrating a wide range of bioactivities, with antibacterial, antiviral, antifungal and antiparasitic effects being particularly notable [6,7,18–20].

The central hypothesis of this review is that the strategic use of probiotics, prebiotics, and phytobiotics can serve as potent and sustainable substitutes to antibiotics and chemotherapeutics in aquaculture by enhancing host health, improving disease resistance

and supporting environmental quality. While several reviews have addressed the use of these agents individually, in specific aquaculture species, extensive studies that bring together natural biotics across diverse aquaculture systems are still lacking. In line with this, the specific objectives of this review are to comprehensively synthesize current knowledge on: (i) the main types of probiotics, prebiotics, and phytobiotics used across aquaculture systems; (ii) their functional effects and underlying mechanisms, whether applied individually or as synergistic combinations, including their effects on growth, feed efficiency, immune defense, pathogen resistance, reproductive performance and antagonistic activities; (iii) their modes of administration and emerging formulations that optimize their efficacy; and (iv) critically evaluate limitations, addressing conflicting results and current research gaps, thereby providing guidance to future investigations. Overall, the review highlights the capacity of these functional additives to support the productivity and general health of aquatic organisms and reduce reliance on antibiotics and other chemical inputs, thereby promoting a more resilient and environmentally responsible industry.

2. Probiotics for Sustainable Aquaculture

According to the World Health Organization (WHO, 2001), probiotics refer to “live microorganisms that, when administered in adequate amounts, confer a health benefit to the host” [21]. Among the most recognized probiotic microorganisms are both Gram-positive and Gram-negative bacterial strains, notably genera such as *Bacillus*, *Phaeobacter*, and various lactic acid bacteria (LAB), including *Lactobacillus*, *Lactococcus*, and *Enterococcus* [22,23]. These bacteria, typically acknowledged as safe, can generate natural bioactive substances that are linked to various biological functions [8,24]. In addition to bacteria, yeasts are also being examined as probiotics within the aquaculture sector (Table 1). Moreover, bacteriophages and unicellular algae are being investigated for their potential health advantages in aquaculture [6,8,25–27]. In general, probiotics exert direct biocontrol mechanisms through competitive exclusion of pathogens, promotion of antimicrobial substance production, while indirectly influencing host immunity and physiology by stimulating immune response, enhancing growth and survival rates, and modulating microbiota (Figure 1). In aquaculture, these microorganisms enhance the health of cultured species while also aiding in the maintenance of water quality and ensuring the safety of consumers [6].

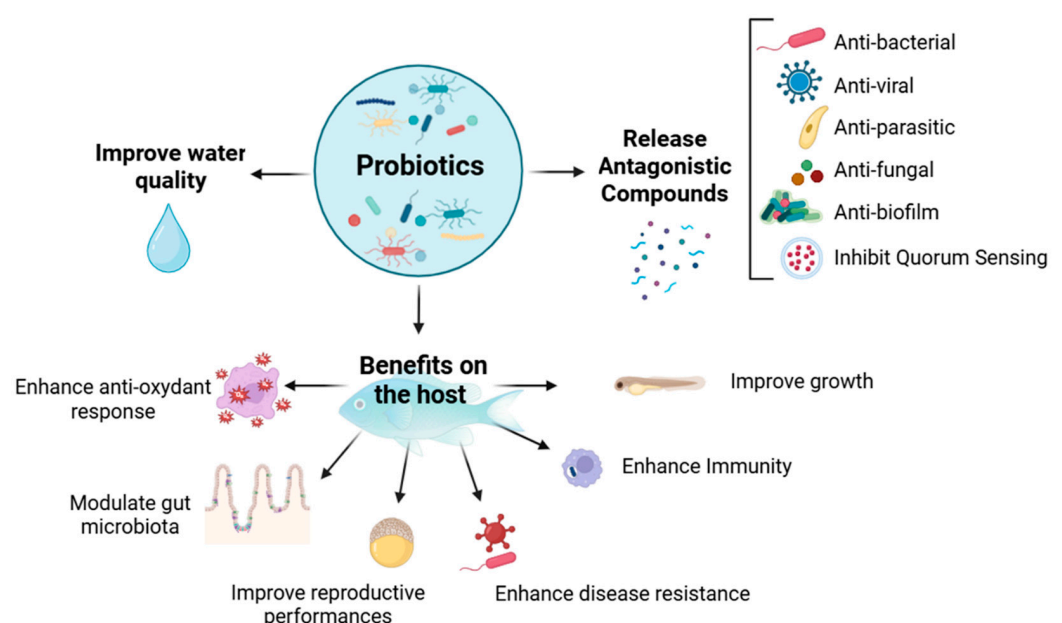


Figure 1. Functional roles of probiotics in aquaculture.

2.1. Effects on Growth and Feed Utilization

Probiotic supplementation has been shown in many studies to positively modulate growth performances, including improvements in final body weight (FBW), weight gain (WG), and specific growth rate (SGR) [28,29]. It would also enhance feed utilization by modulating the gut environment, thereby stimulating the development and function of beneficial autochthonous bacteria. This modulation would support the production of digestive enzymes, including amylases, proteases, and lipases, facilitate the synthesis of essential nutrients, including vitamins, fatty acids, and amino acids, and contribute to the detoxification of harmful dietary compounds. They could also modulate growth biomarkers, particularly insulin-like growth factor-1 (IGF-1) and growth hormone (GH) [6,30,31]. However, the ability of probiotics to modulate digestion and microbiota in aquaculture animals appears to be species dependent and strongly influenced by host physiology and environmental conditions [14,28].

2.2. Effects on Immunity and Disease Resistance

The addition of probiotics to the diets of aquatic species has been shown to improve both cellular and humoral immune responses mediated by various mechanisms, including the stimulation of pro-inflammatory cytokines like interleukin-1 β (IL-1 β) and interleukin-8 (IL-8), tumor necrosis factor-alpha (TNF- α), and transforming growth factor-beta (TGF- β). They would also play an essential role in stimulating natural killer cell activity, increasing the synthesis of mucosal and systemic antibodies, activating phagocytic activity, and raising levels of lysozyme, peroxidase, phenoloxidase (PO), bactericidal and complement activities. Furthermore, probiotics seem to help promote respiratory burst and superoxide anion generation, as well as raise the numbers of macrophages, lymphocytes, erythrocytes, and granulocytes [29,32,33]. These immune-stimulating properties are acknowledged as a key factor in preventing infectious diseases in aquatic species. Probiotics generate functional compounds, namely antibiotics, bacteriocins, siderophores, enzymes, hydrogen peroxide, and organic acids, with reported bactericidal effects against harmful intestinal bacteria, thereby providing a defense against the expansion of opportunistic pathogens and strengthening disease resistance [30]. Furthermore, probiotics may reduce the growth of pathogenic microorganisms both in the gut and on the outer surfaces present in the surrounding culture system [6].

2.3. Effects on Reproductive Performances

Several studies reported that probiotic supplementation may improve reproductive performance in aquatic species through various mechanisms, including increased egg production and size, enhanced production of high-quality eggs, and higher working and relative fecundities, fertilization rates, and hatching rates [34,35]. A positive influence on the gonadosomatic index, overall fecundity, egg viability, and production of healthy fry has also been observed [6,35].

2.4. Effects on the Antioxidative Response

Aquatic animals are commonly subjected to multiple stressors like stocking density, transportation, nutritional deficiency, culture temperature, anoxic and hypoxic stress, hyperoxia, chemicals, pesticides, and fluctuations in water salinity, all of which can significantly impair their physiological condition and exacerbate oxidative stress by stimulating excessive production of reactive oxygen species [30,36]. Probiotics have demonstrated considerable potential to enhance antioxidant status through several mechanisms. They can improve the bioavailability and assimilation of dietary antioxidant compounds, which positively affects organism welfare and reduces oxidative stress [30,36]. By inhibiting

pathogenic bacteria, probiotics also help in the regulation of the gut microbiota, thereby promoting a stable and beneficial microbial community [36]. Certain probiotic strains can generate antioxidant metabolic products such as glutathione, butyrate, folic acid, and extracellular polysaccharides. They would therefore improve the host's antioxidant status by increasing the function of important antioxidant defense enzymes such as catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX), and reduced glutathione (GSH), while simultaneously reducing malondialdehyde (MDA) levels, which further contributes to the overall antioxidant defense system of the host [35,37].

2.5. Effects on Water Quality

In aquaculture practices, water quality can be affected by the accumulation of metabolic products, the decomposition of unused feed and the deterioration of different biotic materials [6]. These processes can compromise water quality parameters like temperature, pH, ammonia concentration, carbon dioxide, and iron levels, which substantially trigger behavioral shifts, leading to physiological consequences and changes in morphometric traits of organisms and creating favorable conditions for pathogen proliferation and thereby increasing susceptibility to disease, all of which affect the welfare and productivity of aquatic organisms [38,39]. The application of probiotics directly in the rearing water can be used throughout all developmental stages of cultured species [40]. Although the specific mechanisms through which probiotics exert their effects in aquatic ecosystems remain inadequately elucidated, several studies reported that probiotics can contribute to the management of aquatic water conditions by increasing the degradation of organic matter; mitigating nitrogen and phosphorus concentrations; regulating nitrite, ammonia, and hydrogen sulfide levels; reducing the proliferation of harmful phytoplankton and bacterial pathogens, and promoting the bioremediation of organic pollutants in cultured water. These water quality improvements may contribute to a more stable habitat, which can indirectly enhance the health of aquatic animals and help maintain balanced interactions between organisms and their environment in aquaculture systems [30,32,39]. For example, *Bacillus* species are considered to be effective water probiotics due to their high resistance to water conditions, their capacity for bioremediation, and their ability to suppress pathogens while promoting the growth of beneficial microbial communities [39].

2.6. Antagonistic Effects

Probiotics produce a variety of bioactive compounds that can modulate receptor and enzyme functions, such as inhibition or induction, and they exhibit a wide range of biological activities [41]. In aquaculture, many aquatic probiotics have been reported to release a broad spectrum of bioactive molecules that enhance the health of aquatic animals through diverse activities, including antimicrobial, anti-biofilm, antioxidant, immunostimulant, and anti-inflammatory effects, as well as the inhibition of pathogen quorum-sensing (QS) systems [18,19,42].

For example, probiotics produce specific narrow-spectrum toxins, such as bacteriocins and bacteriocin inhibitors, to protect themselves from their effects [43]. Probiotics are also a source of organic acids, hydrogen peroxide, carbon dioxide, and siderophores [19,44], short-chain fatty acids (SCFAs)—primarily propionic, acetic and butyric acids—as well as small peptides, amino acids, phenols, lactones, and indoles. These substances help maintain energy balance and exert antioxidant and anti-inflammatory activities, while also enhancing resistance to pathogens through immune signaling. To support metabolism, probiotics also synthesize enzymes such as proteases, lipases, esterases, and amylases, which may be insufficient in the host, as well as β -galactosidase and lactase [43].

Microalgae, as unicellular photoautotrophic microorganisms, produce a wide range of metabolites comprising polyunsaturated fatty acids, proteins, polysaccharides, vitamins, phenolics, and sterols, as well as pigments such as chlorophylls, carotenoids, and phycobilins [45]. These metabolites exhibit a range of biological activities, including antioxidant, anti-inflammatory, and antimicrobial properties, all of which could enhance immune defenses in aquatic species.

2.6.1. Antibacterial Effects

Bacterial diseases have become a major obstacle in aquaculture, as bacteria are well-adapted to survive independently in aquatic environments, particularly under warm water conditions [46]. In response, probiotics are widely recognized in aquaculture for their antibacterial properties against known pathogens [19]. Various microorganisms, including LAB, *Bacillus* spp., *Actinobacteria*, as well as yeasts, have demonstrated antibacterial activity against several aquatic pathogens [47]. For instance, *Bacillus velezensis* FS26 exhibited strong antimicrobial properties against *Aeromonas hydrophila* LMG 13658 and *Aeromonas veronii* clone DK-A. *veronii*-27 [48].

2.6.2. Antiviral Effects

Probiotics are recognized for their potential to decrease the incidence of viral infections in aquaculture due to their antiviral activity [49]. However, the exact mechanisms underlying these effects remain largely unknown. Previous studies suggest that bioactive substances, such as bioactive extracts from marine algae and bacterial extracellular products, can inactivate viruses [50]. More recently, probiotics have demonstrated their ability to enhance resistance in shellfish against viral infections. For example, *Bacillus* spp. and LAB mitigate mortality resulting from white spot syndrome virus (WSSV) and yellow head virus (YHV) infections [51]. Furthermore, ethyl acetate extracts from the supernatant of *Bacillus velezensis* JW inhibited the replication of spring viremia of carp virus (SVCV) in vitro as well as in vivo [52]. Additionally, *Bacillus subtilis* and its secreted lipopeptide surfactin, exhibited antiviral activity in defense of viral hemorrhagic septicemia virus (VHSV) in olive flounder [53].

2.6.3. Antifungal Effects

The antifungal properties of probiotics have also been documented. *Burkholderia strain* HD05, isolated from a freshwater environment, exhibited strong antifungal activity, primarily through the extracellular metabolite 2-pyrrolidone-5-carboxylic acid, which was characterized as the main active compound responsible for reducing hyphal development and spore germination of *Saprolegnia* spp. This fungus is among the most commonly detected pathogens causing saprolegniasis outbreaks in freshwater aquaculture [54]. In another study, soil-derived *Bacillus* sp. strain BC01 considerably reduced the mycelial growth of the fish pathogen, *Aphanomyces invadans* in vitro [55].

2.6.4. Antiparasitic Effects

The potential of probiotics to influence the course of parasitic infections has been widely investigated [56]. In aquaculture, dietary inclusion of live yeast *Debaryomyces hansenii* strain CBS 8339 conferred protection against *Amyloodinium ocellatum* by stimulating humoral and antioxidant immune responses in juvenile *Myxoterperca rosacea*, thereby enhancing resistance to infection [57]. Similarly, Abdel-Aziz et al. (2020) reported that dietary administration with beneficial probiotic microorganisms resulted in partial protection against *Trichodina* protozoan parasite challenges in Nile tilapia (*Oreochromis niloticus*) [42].

2.6.5. Antibiofilm Activity

Biofilms are groups of various microorganisms that are enclosed in their own synthesized extracellular polymers and attached to living or non-living surfaces. This matrix consists of polysaccharides, proteins, lipids, teichoic acids, alginate, extracellular DNA, as well as additional organic compounds produced by bacteria or obtained from the environment. Biofilm formation is a critical determinant of pathogen virulence, promoting their persistence and being associated with severe chronic infections [58,59]. Many probiotics have been shown to have the ability to inhibit biofilm formation [60–62]. In aquaculture, the epiphytic marine bacterium *Staphylococcus lentus* inhibited biofilm formation of *Vibrio harveyi* under co-culture conditions [63]. Another study showed that silver nanoparticles coated with cell-free extracts of *Bacillus licheniformis* exhibited strong anti-biofilm activity against *Vibrio parahaemolyticus* Dav1 [64].

2.6.6. Inhibition of Quorum Sensing

QS is a bacterial regulatory, signaling mechanism that enables bacterial communication based on population density through small signaling molecules known as auto-inducers [19,59]. This mechanism regulates biosynthesis of a range of biological macromolecules, including virulence factors, namely, lytic enzymes, biofilm formations, extracellular polysaccharides, and secretion systems [19,65]. Disruption of pathogens' QS system, referred to as quorum quenching (QQ), has emerged as a potential anti-infective approach in aquaculture [19] (Figure 2). Although the production of QQ molecules is predominantly associated with Gram-negative bacteria, it has also been observed in certain Gram-positive species, particularly within the genus *Bacillus*. *Bacillus* spp. have been thoroughly investigated not only for their probiotic traits but also for their ability to produce QQ molecules [65]. These molecules act mainly through enzymatic mechanisms that interfere with QS signaling, thereby reducing pathogen virulence and biofilm formation [66]. Santos et al. (2021) demonstrated that QQ molecules produced by *B. subtilis*, *Bacillus. velezensis*, and *Bacillus pumilus* degraded QS molecules of fish pathogens such as *Aeromonas veronii* and *Edwardsiella Tarda* [65]. Additionally, Chu et al. (2011) reported that the *Bacillus* sp. strain, QSI-1, derived from the fish intestinal tract, effectively degraded acyl-homoserine lactones (AHLs) and reduced extracellular protease activity in *Aeromonas hydrophila* YJ-1 [67]. The biodegradation of AHLs, which constitute the principal family of QS auto-inducers, represents an effective approach for disrupting QS-mediated pathogenicity [19].

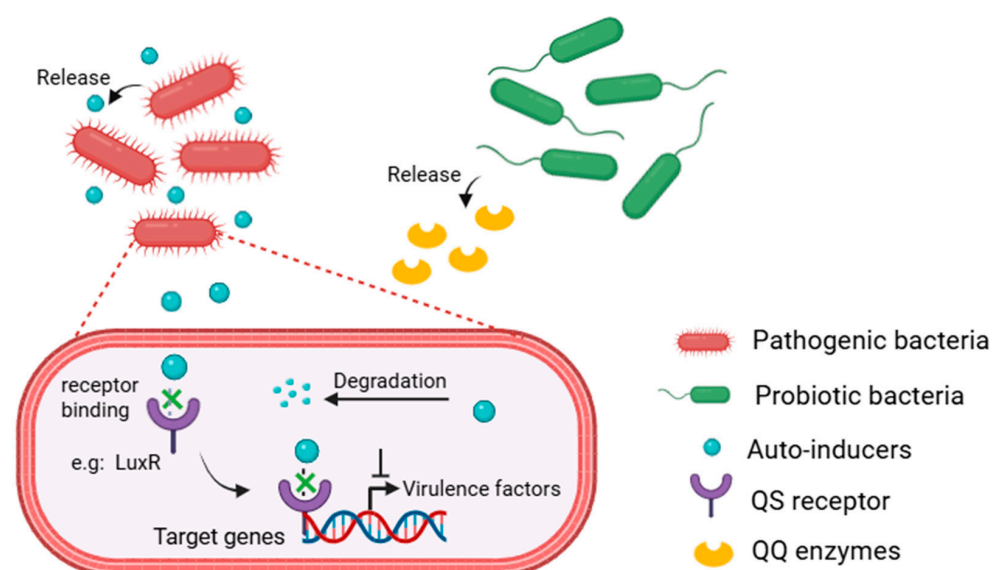


Figure 2. Quorum-sensing inhibition by probiotic bacteria.

Table 1. Beneficial effects of some probiotics in aquaculture.

Type of Microorganism	Probiotic Strains	Dosage	Duration	Temperature	Aquatic Species	Beneficial Effect on the Host	References
Bacteria	Lactic acid bacteria (<i>Lactobacillus plantarum</i> and <i>Lactobacillus fermentum</i>)	10 ⁸ CFU/g diet	38 days	7.6 °C	Atlantic salmon (<i>Salmo salar</i>)	Increased concentration of acetoacetic acid, succinic acid, and total SCFAs	[68]
						High expression of defensin1 in the skin in the treatment with <i>L. plantarum</i>	
						Increased number of gill mucous cells	
						Reduced the width of the lamina propria	
	<i>Bacillus subtilis</i>	5 g/kg diet	30 days	-	Whiteleg shrimp (<i>Penaeus vannamei</i>)	Elevated intestine supranuclear vacuoles	[29]
						Increased weight gain, muscle crude protein content, and enzyme indexes (α -amylase, PO, SOD)	
Bacteria	<i>Lactobacillus casei</i>	10 ⁷ CFU/g diet	75 days	-	Zebrafish (<i>Danio rerio</i>)	Improved the composition of the intestinal flora	[69]
						Increased the total protein, total globulin and lysozyme	
	Commercial probiotics	1.5 g/kg and 3 g/kg diet	60 days	≈27 °C	Nile tilapia (<i>Oreochromis niloticus</i>)	Improved growth, reproductive performances and immune responses by the increase in gene expression of IGF-1, GH, TNF- α , lysozyme, follicle-stimulating hormone receptor, androgen receptor, and Activin	[40]
						Improved FBW, WG and SGR	
						Increased expression of intestinal caspase-3 and proliferating cell nuclear antigen	
	<i>Enterococcus faecium</i>	8.55 × 10 ⁶ CFU/g of body weight	40 days	18 °C	Big-belly seahorses (<i>Hippocampus abdominalis</i>)	Increased pro-inflammatory gene expression (TNF- α , IL-1 β) and anti-inflammatory cytokines (IL-10, TGF- β)	[70]
						Improved growth performance	
						Increased expression of intestinal immune-related genes	
						Increased survival rate against pathogenic <i>Edwardsiella tarda</i> exposure	

Table 1. Cont.

Type of Microorganism	Probiotic Strains	Dosage	Duration	Temperature	Aquatic Species	Beneficial Effect on the Host	References
Yeasts	<i>Saccharomyces cerevisiae</i>	20 g/kg diet	84 days	25.5 °C	Channel catfish (<i>Ictalurus punctatus</i>)	Improved growth, intestinal health and liver function Enhanced disease resistance after challenge with mixed infection of <i>A. veronii</i> HM091 and <i>A. hydrophila</i> NJ-1	[71]
	<i>Kluyveromyces lactis</i> M3	5.5 g/kg and 11 g/kg diet	30 days	20 °C	Gilthead seabream (<i>Sparus aurata</i>)	Modulated structure of intestinal microbiota Immunostimulant activity Enhanced bactericidal activity against <i>V. parahaemolyticus</i> N16, <i>V. harveyi</i> Lg 16/00, and <i>Vibrio anguillarum</i> CECT 43442	[72]
	Commercial baker's yeast, <i>S. cerevisiae</i>	1 g/kg diet	75 days	-	Catfish gulsha tengra, (<i>Mystus cavasius</i>)	Improved growth, feed utilization and disease resistance after challenge with <i>Pseudomonas fluorescens</i>	[73]

Where necessary, values were converted from the units reported in the original references to allow comparison. GH: growth hormone, FBW: final body weight, SGR: specific growth rate, WG: weight gain, IGF-1: insulin-like growth factor-1, IL: interleukin, PO: phenoloxidase, SCFAs: short-chain fatty acids, SOD: superoxide dismutase, TNF- α : tumor necrosis factor-alpha, TGF- β : transforming growth factor-beta.

3. Prebiotics for Sustainable Aquaculture

Prebiotics are substrates selectively utilized by the host microbiome to promote host health [74–76]. Dietary prebiotics must withstand hydrolysis by gastric secretion and host enzymes and be absorbed in the gastrointestinal tract [74,77]. In addition, they must be fermentable by the gut microbiota and enhance the proliferation and/or function of beneficial bacteria, including *Bifidobacteria* and *Lactobacillus*. This stimulation may reduce the abundance of pathogenic bacteria in the digestive system and/or regulate the production of beneficial bacterial metabolites [74,76,77]. Common prebiotics are indigestible carbohydrates, which can be classified as monosaccharides, oligosaccharides, or polysaccharides in relation to their molecular size or polymerization degree [76]. However, some non-carbohydrate compounds, such as flavanols, can also meet the criteria for prebiotics [77]. Prebiotics are found naturally in a range of dietary food products such as fruits, legumes, vegetables, or milk, but also in microalgae and seaweed [6,74,75,77].

Galactooligosaccharides (GOS), fructooligosaccharides (FOS), arabinoxylan-oligosaccharides (AXOS), oligosaccharides, inulin, and β -glucan are some of the most commonly used prebiotics in aquaculture (Table 2) [6,74]. Many investigations have focused on the role of prebiotics in influencing the intestinal microbiota of finfish and crustaceans [78]. Thus, prebiotics have been reported to act as biocontrol agents by indirect mechanisms, allowing for the promotion of growth performance, survival, and nutrient digestibility, increasing feed utilization, improving overall health status, enhancing immune defenses, modulating gut microbiota, and stimulating resistance to diseases in aquaculture [6]. Nevertheless, these effects are not universal, as the host gut microbiota exhibits selectivity towards specific prebiotics [74]. This specificity is largely determined by several factors, including host conditions, type and inclusion level of the prebiotic, structural characteristics,

such as degree of polymerization and chemical composition, and the enzymatic capabilities of beneficial bacteria to hydrolyze these compounds [79,80].

Supplementation with prebiotics has been demonstrated to positively affect growth and feeding performances in aquatic species by stimulating digestive enzyme activity, including protease, amylase, lipase, cellulase, phytase, tannase, xylanase, and chitinase, as well as by altering intestinal morphology and promoting the metabolic processing of prebiotic compounds by health-promoting intestinal microbes [6].

Some authors refer to prebiotics that stimulate the immune system of an organism as immunosaccharides. Recognized immunostimulant prebiotics include FOS, GOS, mannanoligosaccharides (MOS), xylooligosaccharides (XOS), and inulin [80–83], and the homopolysaccharide β -glucan, which is the most extensively used, either individually or in combination with other prebiotics to enhance the immune response in both marine and freshwater aquaculture species [74]. The immunomodulatory effects of prebiotics are mediated either indirectly, by promoting the development of beneficial indigenous microbiota, or directly, by activating the innate immune system through direct interactions with the pattern recognition receptors (PRR) expressed on the surface of the host cell, e.g., β -glucan and dectin-1 receptors. These interactions can activate intracellular signaling pathways, including nuclear factor kappa B (NF- κ B), as well as signaling molecules like extracellular signal-regulated kinase (ERK) often through adaptor molecules such as myeloid differentiation primary response 88 (MyD88), and the modulation of the expression of apoptosis-related regulators such as B-cell lymphoma-2 (Bcl-2), ultimately resulting in the stimulation of immune cells and the enhancement of the innate immune response [83–85]. Prebiotics directly enhance non-specific immunity through various mechanisms, including the elevated phagocytic, neutrophil, and lysozyme activity, as well as the activation of the alternative complement system [6,84]. Therefore, based on the potential health benefits provided by prebiotics in aquatic species, the productivity and sustainability of aquaculture systems might be increased using prebiotics [76].

Table 2. Effects of common dietary prebiotics on various aquatic species.

Prebiotic	Dosage	Duration	Temperature	Aquatic Species	Beneficial Effect on the Host	References
β -Glucan + oligosaccharides	1.5 g/kg and 2 g/kg diet	60 days	26 °C	Nile tilapia (<i>Oreochromis niloticus</i>)	Improved feed efficiency	[86]
					Increased survival rates	
					Enhanced body composition	
					Up-regulation of growth-related genes (GH, IGF-1)	
GOS	30 g/kg diet	56 days	$\approx$ 16 °C	Juvenile hybrid sturgeon (<i>Acipenser baerii</i> female crossed with <i>A. schrenckii</i> male)	Improved growth performance	[82]
					Enhanced antioxidant capacity and immune response	
					Improved intestinal morphology	
					Increased disease resistance	

Table 2. Cont.

Prebiotic	Dosage	Duration	Temperature	Aquatic Species	Beneficial Effect on the Host	References
FOS	4 g/kg diet	63 days	25 °C	Blunt snout bream (<i>Megalobrama amblycephala</i>)	Improved growth performance	[83]
					Enhanced antioxidant capacity and immune response	
					Improved intestinal morphology	
					Increased disease resistance	
					Enhanced antioxidant capacity by the upregulation of SOD and CAT	
Commercial prebiotic (MOS + β -glucan)	15 g/kg diet	90 days	28 °C	Shabout (<i>Tor grypus</i>)	Improved liver morphology and reduced necrosis caused by <i>A. hydrophila</i> infection.	[81]
					Regulation of apoptotic genes (up-regulation of caspase-8 and caspase-9 and down-regulation of Bcl-2).	
					Reduction in inflammatory responses	
					Enhanced innate immune response (enhancement of lysozyme and bactericidal activity)	
					Upregulation of IL-1 β , IL-8, and TNF- α in the head kidney.	
GOS + inulin	5 g/kg GOS and 5 g/kg inulin diet	56 days	16.5 °C 20 °C 30 °C	Chu's croaker (<i>Nibea coibor</i>)	Improved growth performance and immune response	[80,82]
					Enhanced antioxidant capacity	
					Modulation of intestinal microbiota and SCFA production	
XOS	5 to 10 g/kg diet	56 days	12–13 °C	Triploid rainbow trout (<i>Oncorhynchus mykiss</i>)	Improved growth performance (WG, SGR)	[87]
					Enhanced digestive enzyme activity (lipase, amylase)	
					Improved intestinal histology	
					Regulation of inflammatory cytokines and microbiota	
AXOS + inulin	4 g/kg diet	56 days	28 °C	Pacific white shrimp (<i>Litopenaeus vannamei</i>)	Enhanced growth parameters (SGR, average daily gain, feed conversion ratio)	[85]
					Upregulation of growth-related genes (chitinase, cathepsin L, chymotrypsin, ERK)	
					Modulation of gut microbiota	
					Improved immune response (enhancement of MyD88 and PO expression)	

Units were standardized by the authors to ensure consistency across studies. GOS: Galactooligosaccharides, FOS: fructooligosaccharides, AXOS: arabinoxylan-oligosaccharides, XOS: xylooligosaccharides. GH: growth hormone, IGF-1: insulin-like growth factor 1, SOD: superoxide dismutase, CAT: catalase, IL: interleukin, TNF- α : tumor necrosis factor- α , SCFA: short-chain fatty acids, SGR: specific growth rate, WG: weight gain, ERK: extracellular signal-regulated kinase, MyD88: myeloid differentiation primary response 88, PO: phenoloxidase, Bcl-2: b-cell lymphoma 2.

4. Phytobiotics for Sustainable Aquaculture

Phytobiotics are plant-based immunostimulants that act as biocontrol agents directly by releasing bioactive substances, in particular polysaccharides, phenolics, terpenoids, tannins, saponins, sulphur, flavonoids, glycosides, and steroids. These compounds exhibit several biological properties, including antibacterial, antiviral, antifungal, antihelminthic, antiparasitic and antioxidant effects (Figure 3) [88,89]. They can exert indirect immunomodulatory effects, enhance disease resistance [88], and improve productive parameters through the stimulation of saliva and bile secretion. Moreover, some phytobiotics act as prebiotics by providing specific substrates that support beneficial intestinal microbiota, thereby reducing the risk of pathogenic bacterial colonization [90]. In aquaculture, a wide variety of plants and their secondary products serve as rich sources of phytobiotics, including medicinal plants, spices, mushrooms, fruits, vegetables, seeds, nuts, essential oils, and marine resources, such as microalgae and seaweed [15].

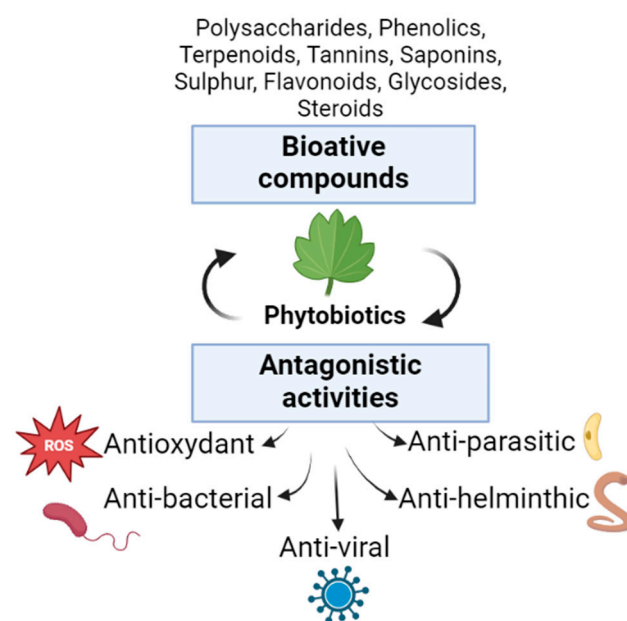


Figure 3. Bioactive compounds released by phytobiotics and their potential antagonistic activities.

Extracts from over 60 different medicinal plant species have been identified and utilized to improve fish health [90]. These plant-derived compounds have been observed to boost immune responses, stimulate appetite, promote growth, increase reproductive performances and sexual parameters of aquatic species, as well as contribute to improved water quality [89,91]. However, the observed effects are influenced by several factors such as plant source, phytochemical composition, specific bioactive compounds, as well as species-specific and dose-dependent responses [15,89,92].

The major plant species with the highest potential for application in aquaculture include garlic (*Allium sativum*), turmeric (*Curcuma longa*), neem (*Azadirachta indica*), ginger (*Zingiber officinale*), Malaysian ginseng (*Eurycoma longifolia*), indian ginseng (*Whitania somnifera*), Aloe (*Aloe vera*) and licorice (*Glycyrrhiza glabra*) (Table 3) [7,15,92].

In addition, other plant extracts have been demonstrated to exert a range of health-promoting functions on aquatic organisms. For instance, dietary chia (*Salvia hispanica*) seed powder enhanced growth and immune defense in Nile tilapia (*Oreochromis niloticus*) by improving hematological antioxidant and immune indices [93]. Similarly, dietary inclusion of *Papaveraceae* extract improved growth performance and feed utilization in striped catfish (*Pangasianodon hypophthalmus*) while also enhancing serum biochemical indices following *Aeromonas hydrophila* infection [91]. Moreover, a wide variety of microalgae and

macroalgae are rich sources of secondary metabolites and bioactive compounds, which exhibit diverse bioactivities that contribute to overall health promotion and increased disease resistance in aquatic species [7,15]. For example, dietary supplementation with red macroalgae (*Halopithys incurva*) enhanced immune and antioxidant defenses in zebrafish (*Danio rerio*) [94].

Table 3. Health promoting effects of common plants in aquatic species.

Plant Species	Dosage	Duration	Water Temperature	Aquatic Species	Beneficial Effect on the Host	References
Garlic (<i>Allium sativum</i>)	20 g/kg	90 days	25 °C	Narrow-clawed crayfish (<i>Postantacus leptodactylus</i>)	Improved growth performance, Enhanced digestive enzymes activity (amylase and protease), Enhanced innate immunity (↑ total hemocyte count and lysozyme activity)	[95]
Ginger (<i>Zingiber officinale</i>)	2 g/kg	60 days	27.5 °C	Common Carp (<i>Cyprinus carpio</i>)	Improved antioxidant parameters Improved growth performance Improved hematological parameters Enhanced serum parameters (Total protein, albumin, globulin, lysozyme, SOD, CAT and Immunoglobulin)	[96]
Indian ginseng (<i>Withania somnifera</i>)	2 g/kg of feed	56 days	28 °C	White-leg shrimp (<i>Litopenaeus vannamei</i>)	Improved immune system and antioxidant status Improved growth and digestion Enhanced antioxidant biomarkers (SOD, CAT and GPx) Improved immune response (↑ THC, TP, lysozyme, phagocytic activity) Resistance to <i>Vibrio harveyi</i>	[97]
Turmeric (<i>Curcuma longa</i>)	10 g/kg	56 days	27.8–28.2 °C	Nile tilapia (<i>Oreochromis niloticus</i>)	Enhanced feed utilization Improved immune response (↑ respiratory burst activity and lysozyme) Resistance to <i>Streptococcus agalactiae</i>	[98]
Neem (<i>Azadirachta indica</i>)	1 g/kg and 2 g/kg	60 days	28.1–29.5 °C	Nile tilapia juveniles (<i>Oreochromis niloticus</i>)	Improved growth performance Enhanced digestive enzymes and intestinal morphology Improved immunological activities (↑ lysozyme, complement C3, Nitric oxide) Enhanced antioxidant enzymes (CAT, SOD, and GPX)	[99]
<i>Eurycoma longifolia</i>	16 g/kg	42 days	-	White-leg shrimp (<i>Litopenaeus vannamei</i>)	Resistance to <i>A. hydrophila</i> and <i>C. tilapia</i> Enhanced immune response (↑ PO, Total hemocyte count and respiratory burst) Increased disease resistance	[100]

Table 3. Cont.

Plant Species	Dosage	Duration	Water Temperature	Aquatic Species	Beneficial Effect on the Host	References
<i>Aloe vera</i>	30 g/kg	70 days	24.8–28.6 °C	Mori fish (<i>catla</i>)	Improved growth (WG, Feed conversion ratio, survival rate)	[101]
					Improved digestibility (↑ Gross energy, crude protein and crude fat)	
					Improved hematological parameters	
					Increased antioxidant activity (CAT, SOD, and GPX)	
					Enhanced immune response	
Licorice (<i>Glycyrrhiza uralensis</i>)	4 g/kg	105 days	28 °C	Common carp (<i>Cyprinus carpio haematopterus</i>)	Improved growth performance (FBW, WG, SGR, protein efficiency ratio)	[102]
					Increased the content of crude protein and improved the composition of amino acids and fatty acids.	
					Improved non-specific immunity and antioxidant activity	
					Regulation of serum indices (↓ Triglycerides, Total cholesterol and ↑ High-density lipoprotein)	

Units were standardized by the authors to ensure consistency across studies. SOD: superoxide dismutase, CAT: catalase, GPx: glutathione peroxidase, PO: phenoloxidase, SGR: specific growth rate, WG: weight gain, FBW: final body weight. ↑: increased, ↓: decreased.

5. The Concept of Synbiotics in Aquaculture

Synbiotics are dietary supplements that synergistically combine probiotics and prebiotics to enhance the beneficial effects of each component [103,104]. In recent years, the combination of probiotics and plant-derived components has gained increasing importance due to its positive effects on the overall condition of aquatic organisms [105].

Synbiotics can improve the host's health by selectively promoting the growth and/or metabolic functions of one or more beneficial bacteria, which may promote the survival and absorption of microbial supplements in the gastrointestinal system, depending on the host, environmental conditions and diet composition [74,106].

The effects of synbiotics can generally be categorized into three types: additive effect (the combined effect equals the cumulative effect of individual components), synergistic effect (wherein the cumulative effect of the two components surpasses the aggregate of the individual effects of the components) and enhancing effect, a term used to describe super-synergistic effects or effects that occur exclusively when the two compounds are administered concurrently [107].

Based on the synergistic compatibility between probiotic strains and prebiotic substrates, numerous studies have demonstrated that synbiotic inclusion may enhance the growth, feed efficiency ratio, digestive enzymatic activity, immune function, and disease resistance of aquatic organisms [104,108]. For example, in tilapia (*Labeo rohita*) infected with *Aeromonas hydrophila*, the addition of *Bacillus subtilis* and GOS to the feed can improve antioxidant activity, innate and adaptive immune reactions, reduce mortality, and regulate the expression of immune-related cytokine genes [109]. Similarly, the combination of *Lactobacillus acidophilus* and *Moringa* leaf extract can improve the growth, immune parameters, and resistance to *Vibrio alginolyticus* and *Vibrio parahaemolyticus* in *Penaeus vannamei* [110].

Recent investigations have also emphasized the potential of combining algae and pure cultured bacteria to form novel symbiotic systems [111]. This bacterial-microalgal

combination has been shown to improve water quality and promote gut health through mechanisms including stimulating the activity of digestive enzymes, improving gut morphology and gut microbiota composition in juvenile crucian carp (*Carassius auratus gibelio*), and ultimately increasing fish yield [112].

6. Modes of Administration of Probiotics, Prebiotics and Phytobiotics

The effective administration of probiotics, prebiotics, and phytobiotics is critical for enhancing host health in aquaculture. The commonly used delivery methods include oral dietary supplementation, addition to water and injection (Figure 4) [7,103,113–115]. The choice of administration method depends on several factors, such as the target species, developmental stage, culture system, and the bioavailability and stability of the compounds involved [15,110,116]. Among these, dietary supplementation, whether incorporated in pellets or live feed, is the most widely adopted method as it ensures targeted delivery to the gastrointestinal tract and has been shown to significantly improve the health of aquatic species. Water administration is another common approach, particularly suitable for early life stages with underdeveloped digestive systems or in systems such as biofloc aquaculture. In this method, probiotics, prebiotics and phytobiotics are added directly to the rearing water to enhance microbial balance and improve water quality [15,111,113]. Although injection is less commonly used for probiotics due to the stress it can induce in aquatic animals, it remains an effective method for delivering phytobiotics. However, its application remains limited, as it is not practical for large-scale or routine operations [15].

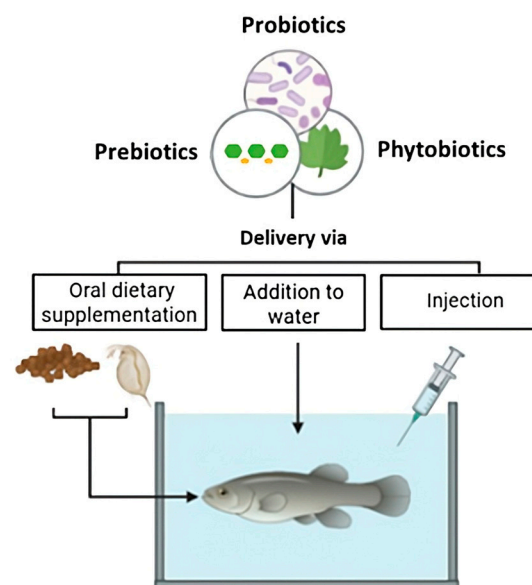


Figure 4. Modes of administration of probiotics, prebiotics and phytobiotics in aquaculture.

Probiotics and prebiotics can be applied in various forms, including powdered, encapsulated, micro-encapsulated, and bio-encapsulated in live feed such as *Artemia*, *Daphnia* or rotifers, which are widely used during early developmental stages [117,118]. Beyond conventional live-cell probiotics, alternative forms have also emerged [78]. These include heat-inactivated (thermally killed) probiotics, which can still confer immunostimulatory effects without the risk of microbial overgrowth [78], and spore-forming probiotics, such as those from *Bacillus* spp., which are highly resilient to environmental stress and feed processing conditions [115]. Additionally, postbiotics-non-viable probiotic products including metabolic byproducts, cell wall fragments, and extracellular polysaccharides have demonstrated potential in modulating host immunity and gut health [119]. Ultrasonically disrupted probiotics, which release intracellular components with potential bioactivity,

have recently gained attention as a novel approach in functional feed formulations [6]. Regarding phytobiotics, plants can be applied as a whole or as a specific part, such as leaves, roots, seeds, or fruits. They can be used fresh or as an herbal extract prepared with various solvents, including water, methanol, chloroform, and ethyl acetate [7].

7. Limitation, Conflicting Results and Research Gaps

The integration of probiotics, prebiotics and phytobiotics has been widely demonstrated to be effective in aquaculture systems. Their incorporation into feed and water has proven their ability to improve growth performances, enhance immune function, increase disease resistance, modulate intestinal microbiota and improve water quality. Despite these benefits, their application in aquaculture is linked to several issues. Probiotic strains isolated from different sources can exert distinct, strain-specific effects in improving host health [120]. Additionally, while many probiotics applied in aquaculture originate from terrestrial sources, research suggests that host-associated probiotics are more appropriate for aquaculture use, as they contribute to host defense mechanisms and are better adapted to survive in these environments, where the gastrointestinal tract of aquatic organisms is constantly exposed to water and fluctuating environmental conditions [121]. Hence, the appropriate selection of probiotic strains is an essential factor in ensuring their effectiveness. The stability of probiotics in feed formulations is another critical factor for their efficacy, as the viability of the probiotic can be altered by moisture content, temperature and oxidation levels [122]. Consequently, storage conditions must be controlled. In addition, the development of novel strategies such as encapsulation techniques or the use of more stable forms of probiotics, including spore-forming *Bacillus* strains, should be taken into consideration [1].

Another major challenge in the application of probiotics is their host specificity, as individual responses can vary depending on the host's physiological conditions, environment, genetics, and microbiota [14,122,123]. The same bacterial strain might have a beneficial effect on an aquatic animal but may be ineffective or pathogenic for another [32]. Therefore, each probiotic must be selected for the specific target host and culture conditions. Alternatively, probiotics might be chosen for their broad-spectrum effects to ensure consistent benefits across different organisms before their application in aquaculture [122]. Moreover, probiotic feeding dosages and treatment durations are not universal and remain poorly standardized. Probiotic dosages may show different outcomes across hosts depending on their species and their physiological conditions. In addition, optimal dosage is influenced by probiotic strain, the intended application and the rearing system [32,122]. For instance, freshwater and marine species have different physiological features and nutritional preferences, which require the use of tailored strains and doses of probiotics [14]. Most studies use an inclusion level of probiotics within a range of 10^7 – 10^{11} CFU/kg diet, for periods varying between 6 days to more than 5 months [32,124]. Continuous feeding is largely used in experimental studies. However, the long-term effect of persistent use of probiotics remains underexplored, as microbial interactions may impact fish health mainly through disruption of gut microbial balance, which increases the susceptibility to pathogens, posing risks to biodiversity within aquatic ecosystems [31,122,123,125].

Another limitation about the use of probiotics is their risk of containing mobile genetic elements (MGEs) such as prophages, plasmids and insertion sequences that are the main drivers for horizontal gene transfer. This may lead to increased antibiotic resistance, as these determinants can be transferred between pathogenic and non-pathogenic bacteria in aquatic ecosystems. Hence, the selection of probiotics must include an integrated genomic characterization through the identification of virulence factors, antibiotic resistance genes, MGEs, and CRISPR-Cas systems to ensure total safety and environmental sustainability within aquatic habitats [32,126].

The application of prebiotics shows different outcomes, as their efficacy is influenced by several factors, including the type of prebiotics, the host species, ecological conditions and their bioactivity with probiotics that are present in the host gut [74,127]. Similarly, the effects of prebiotics are species-specific. For example, pearl gentian grouper responded differently to different types of prebiotics, showing better overall effects on growth performance, stress resistance and immune response when administered with MOS and XOS compared with FOS, chitosan, and β -glucan [128]. The dosages of prebiotics depend on factors such as the health status of the animals, their body size, and age. When used inappropriately, prebiotics may give adverse effects on gut health, growth and the immune system [127,129]. Additionally, as prebiotics are related to bacterial communities, seasonal temperature fluctuations of aquatic organisms may impact the effectiveness of prebiotics and nutrient digestibility by modulating gut microbiota [129].

Despite the reported advantages of phytobiotics in aquaculture, their effectiveness is inconsistent [130]. This variability is affected by factors including plant species, the extraction method, and the availability of bioactive phytochemicals. In addition, the bioactivity of phytobiotics is affected by environmental conditions, including water quality parameters, which reduce their absorption [89,92,131]. Furthermore, many phytobiotics have been evaluated under experimental conditions, where the quantity of extracts is controlled. However, there is a need to synthesize these functional compounds for evaluation at a large scale [130].

Overall, the regulation of the application of probiotics, prebiotics and phytobiotics in aquaculture is heterogeneous worldwide, and their incorporation may acquire approval. Thus, cooperation among researchers, aquaculture practitioners, feed manufacturers and regulatory authorities is important for the standardization of dosages, and the development of harmonized guidelines across countries is essential to maximize their use while ensuring their safety for aquatic animals, the environment and the consumer [126,129,131,132].

8. Conclusions

Probiotics, prebiotics, and phytobiotics have significant potential to improve growth, stimulate immune defense, and increase resistance to various diseases in aquatic species. Considering their numerous benefits, these bio-friendly feed additives can act as effective substitutes to antibiotics and synthetic drugs, while also promoting the health and welfare of aquatic animals. Consequently, they can help steer aquaculture production toward more sustainable practices. Beyond these general benefits, future research should focus not only on elucidating the precise mechanisms underlying these beneficial effects but also on optimizing dosage, formulation, duration and delivery methods tailored to different species and developmental stages. Additionally, evaluating potential synergistic or antagonistic interactions when these compounds are used in combination is essential to maximize their effectiveness. Moreover, long-term studies are needed to assess any potential adverse effects, horizontal gene transfer, or ecological risks, particularly in intensive and open aquaculture systems. There is also growing interest in understanding strain-specific performance, host-microbiome interactions, and the influence of environmental factors, including water quality and temperature, on the efficacy of these bioactive compounds. Addressing these gaps will enable the integration of probiotics, prebiotics and phytobiotics into a comprehensive health management strategy and substantially reduce reliance on antibiotics and chemicals, thereby contributing to more resilient and sustainable aquaculture systems.

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Abbreviations

The following abbreviations are used in this manuscript:

ARB	Antibiotic-Resistant Bacteria
ARGs	Antibiotic Resistance Genes
WHO	World Health Organization
LAB	Lactic acid bacteria
SCFAs	Short-chain fatty acids
WSSV	White spot syndrome
SVCV	Spring viremia of carp virus
VHSV	Viral hemorrhagic septicemia virus
QS	Quorum sensing
QQ	Quorum quenching
FOS	Fructooligosaccharides
GOS	Galactooligosaccharides
AXOS	Arabinoxylan-oligosaccharide
MOS	Mannan oligosaccharide
PRR	Pattern recognition receptors
XOS	Xylooligosaccharides
MGEs	Mobile Genetic Elements
SOD	Superoxide dismutase
CAT	Catalase
GPx	Glutathione peroxidase
PO	Phenoloxidase
IL	Interleukin
SGR	Specific growth rate
WG	Weight gain
FBW	Final body weight.
GH	Growth hormone
IGF-1	Insulin-like growth factor 1
TNF- α	Tumor necrosis factor-alpha
ERK	Extracellular signal-regulated kinase
MyD88	Myeloid differentiation primary response 88
Bcl-2	B-cell lymphoma 2.
GHR	Growth hormone receptor
TGF- β	Transforming growth factor-beta

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