

Review

Fungi and Actinobacteria: Alternative Probiotics for Sustainable Aquaculture

Koushik Ghosh ^{1,*} , Ramasamy Harikrishnan ², Abhisek Mukhopadhyay ¹ and Einar Ringø ³ 

¹ Aquaculture Laboratory, Department of Zoology, The University of Burdwan, Burdwan 713104, West Bengal, India

² Department of Zoology, Pachaiyappa's College for Men Affiliated to University of Madras, Kanchipuram 631501, Tamil Nadu, India

³ Fisheries and Economics, Faculty of Bioscience, Norwegian College of Fishery Science, UiT the Arctic University of Norway, 9019 Tromsø, Norway; enar.ringo@uit.no

* Correspondence: kghoshbu@gmail.com or kghosh@zoo.buruniv.ac.in

Abstract: Aquatic animals are continually being exposed to stressors under farming conditions, increasing risks to gut health that result in dysbiosis. Since restrictions are imposed on the frequent use of antibiotics in aquaculture, there is emerging demand for economically viable, environmentally safe, and sustainable alternatives for the intensive production of aquaculture species. The application of beneficial microorganisms as probiotics has been suggested and widely practiced in recent times. Bacteria and fungi are ubiquitous microorganisms that can grow in various environments where organic substrates are available. Being rich in nutrients, a fish's aquatic environment and gastrointestinal tract confer a favorable culture milieu for the microorganisms. However, the colonization and probiotic potential of fungi and mycelial bacteria resembling fungi (actinobacteria), either in the culture environment or within the gastrointestinal tracts of fish, have received less emphasis. Apart from bacilli and lactic acid bacteria, as the most conventionally used probiotics in aquaculture, numerous studies have focused on other promising alternatives. Diverse species of yeasts and molds belonging to the kingdom 'Fungi' have been characterized for their prospective roles in nutrition, immunomodulation, and disease prevention in fish. Bioactive compounds such as manno-oligosaccharides and β -glucans are recognized as fungal postbiotics that improve innate immunity and disease resistance in fish. Actinobacteria are known to possess different hydrolytic enzymes and novel secondary metabolites representing their probiotic attributes. The application of these groups in water quality amelioration has also been explored. Thus, this paper presents an overview of the present status of knowledge pertaining to the effects of yeasts (*Candida*, *Cryptococcus*, *Debaryomyces*, *Geotrichum*, *Leucosporidium*, *Pichia*, *Rhodospiridium*, *Rhodotorula*, *Saccharomyces*, *Sporidiobolus*, *Sporobolomyces*, *Trichosporon* and *Yarrowialipolytica*), molds (*Aspergillus* spp.) and actinobacteria (*Streptomyces*) as probiotics in finfish aquaculture, as well as their occurrence within the gastrointestinal tracts of finfish. Furthermore, probiotic mechanisms, selection criteria, and future perspectives on using fungi and actinobacteria as promising probiotics are discussed.



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Key Contribution: The intensification of aquaculture and antibiotics usage has emphasized the need for alternatives to antibiotics, for example, probiotics applications to make aquaculture more environmentally sustainable and economically viable. The most frequently used probiotics in aquaculture are either *Bacillus* spp. or lactic acid bacteria, but numerous studies have indicated the potentiality of other organisms as probiotics. This paper summarizes the current knowledge of the prospects of yeasts, molds and actinobacteria as alternatives to widely used conventional bacterial probiotics.

1. Introduction

Aquaculture is expected to lead the global fish supply within the next decade. However, the intensification of aquatic production has led to a significant increase in infectious diseases and growing inefficiency among the antibiotics used to treat these diseases. Several options are available today, including probiotics, prebiotics, and postbiotics [1]. The use of probiotics as an alternative approach to reduce the opportunity of pathogens to adhere and colonize the larval, fry and juvenile intestine is to modulate the intestinal microbiota with beneficial microorganisms that can be added either to the diet [2] or into the rearing water [3] to facilitate the proportion of health-promoting microorganisms within the gastrointestinal (GI) tract. The advantage of these administration methods is they can easily be implemented during early development stages when vaccination via injection is impractical. Numerous Gram-positive and Gram-negative bacteria are used as probiotics in aquaculture [1,2,4–6]. Although the applications of bacilli and lactic acid bacteria (LAB) are the most conventionally used probiotics, the search for new probiotic strains is essential to combat the latest, emerging pathogens in aquaculture. As a consequence, a range of other microorganisms, including yeasts [7–10], molds [11,12], bacteriophages, unicellular algae, and some non-conventional bacteria [13], have been evaluated for their probiotic potential.

Yeasts are unicellular eukaryotic microorganisms taxonomically placed within the phyla 'Ascomycota' and 'Basidiomycota' within the kingdom 'Fungi' [14]. In their review devoted to yeast as a sustainable feed resource for use in aquaculture, Øverland and Skrede [15] presented information on chemical composition, digestibility in fish, how processing affects digestibility, and effects on growth performance, nitrogen utilization, carcass composition, and fish health. Gatesoupe, Navarrete and Tovar-Ramírez; Tan et al.; Hayatgheib et al.; and Ceseña et al. [7–10,16] discussed information on yeast probiotics in their review. To avoid duplicating with those findings presented in the above reviews, these studies are only briefly mentioned in this review to allow a complete overview. Unlike yeasts, molds are multicellular organisms classified under the kingdom 'Fungi'. The genus *Aspergillus* consists of common molds reported throughout the environment within soil, water or vegetation and thrives as saprophytes. *Aspergillus* spp. are recognized as an essential source of diverse enzymes, e.g., alpha-amylase, protease and glucoamylase [12,17], and have been recommended for use as promising probiotic feed supplements for fish, as well as poultry and livestock [18]. However, studies conducted on fungal probiotics and their potential bioactive compounds are still inadequate, suggesting scope to look for alternative probiotics for use in aquaculture. Morphologically, actinobacteria resemble fungi because of their elongated cells that branch into hyphae. However, actinomycete hyphae can be distinguished from fungal hyphae, as the size of actinomycete hyphae is much smaller than that of fungal hyphae. Marine actinobacteria have long been designated as the chemical factory, and many chemical substances are reported from them [19]. *Streptomyces*, being the most widely studied actinobacteria, have been shown to possess novel secondary metabolites that add a new dimension to microbial natural products [20]. Despite all the significant features of a good probiotic, actinobacteria have hardly been used as probiotics in aquaculture. Recent reports on the efficacy of actinobacteria in realizing multiple applications and their resemblance to the fungal hyphae tempted us to include them in this review for their prospective role in aquaculture.

Understanding the contribution of fungi and actinobacteria as a part of the gut microbiome may improve fish health and nutrition management, as well as the production performance of fish. Thus, the current review presents an overview of yeasts (*Candida*, *Cryptococcus*, *Debaryomyces*, *Geotrichum*, *Leucosporidium*, *Pichia*, *Rhodospiridium*, *Rhodotorula*, *Saccharomyces*, *Sporidiobolus*, *Sporobolomyces*, *Trichosporon* and *Yarrowia lipolytica*), molds (*Aspergillus* spp.) and actinobacteria (*Streptomyces*) as probiotic supplements in aquaculture, with a focus on growth performance, the modulation of the gut microbiota, the gut histology, the effects on the immune system and disease resistance in finfish. However, some reports on shrimp and other aquatic organisms are presented and discussed to give information of vital interest. Furthermore, some general information is provided regarding

selecting and validating the fungal and actinobacterial strains as potential probiotics for their likely use in sustainable aquaculture.

2. Yeasts as Probiotics

Yeasts form a part of the *normal microbiota* in wild and farmed fish, and their role in fish health and nutrition has also been addressed [8]. *Saccharomyces cerevisiae* and the halotolerant *Debaryomyces hansenii* are two of the most popular and widely studied yeast probiotics in fish [21,22]. Yeast probiotics, as whole-cell or sub-cellular components, modulate the immune and antioxidant systems, enhance gut maturation, and improve the survival, as well as the growth, of fish [8,23–26]. Even when accounting for less than 1% of the total microbial isolates in the host, yeasts can represent a significant physiological contribution beyond what has been observed for probiotic bacteria; yeast may have a 100-fold larger cell volume than bacteria [7].

The extensive metabolic potential of the yeasts has been reflected in their ability to produce diverse enzymes. Polyamines secreted by the yeasts are known to be involved in the maturation of the digestive tract of fish larvae [7]. Moreover, some yeast species and their components, such as β -glucans and mannoproteins, were found to stimulate the host's immune response and antioxidant activity. Yeasts can utilize a broad spectrum of simple or complex organic compounds compared to bacteria. Thus, understanding the contribution of yeasts as a part of the gut microbiome may help to improve our knowledge of the probiotic potential of diverse yeast species and the possibility of their use in sustainable aquaculture. This section outlines the current knowledge regarding the use of yeasts as probiotics in aquaculture systems. Table 1 reveals the beneficial effects of yeasts, along with molds and actinobacteria, used as probiotics in aquaculture.

Table 1. Effects of fungi (yeast and mold) and actinobacteria on growth performance and disease resistance in finfish.

Species	Isolated from	Doses and Duration	Finfish Species Investigated	Parameters Investigated	References
<i>Saccharomyces cerevisiae</i> strain NCYC Sc 47 (Biosaf_Sc 47)	Commercial strain	10 ⁶ CFU g ⁻¹ , 31 days	Rainbow trout, fry	↑ brush border enzymes, gut microbiota (inclusive of probiont colonization) → enzymes like alkaline phosphatase (AP), γ -glutamyl-transpeptidase (GGT) and leucine-amino-peptidase N (LAP) activities	[27]
<i>S. cerevisiae</i>	NI	1.0, 1.5 and 2.0%, 214 days	Egyptian African catfish, 24.3 ± 1.4 g	↑ growth performance at 2% inclusion	[28]
<i>S. cerevisiae</i>	Commercial strain	1 g kg ⁻¹ , 8 weeks	Nile tilapia, 0.66 g	↑ growth performance, microvilli length, <i>hsp70</i> expression in intestine and head kidney, intestinal <i>Lactococcus</i> spp. ↓ gut alkaline phosphatase	[29]
<i>S. cerevisiae</i>	Commercial strain	1 g kg ⁻¹ , 8 weeks	Nile tilapia, ~9.8 g	↑ growth performance, microvilli length, <i>hsp70</i> expression in intestine and head kidney and resistance towards <i>A. hydrophila</i> Alleviates negative effects induced via crowding stress ↓ gut alkaline phosphatase	[30]

Table 1. Cont.

Species	Isolated from	Doses and Duration	Finfish Species Investigated	Parameters Investigated	References
<i>S. cerevisiae</i>	Commercial strain donated by Jastbolaget AB, Sollentuna, Sweden	~log 8 of yeast per g, 6 weeks	Rainbow trout, ~130 g	Yeast-fed fish revealed similar bacterial diversity and lower abundances of Leuconostocaceae and Photobacterium compared to fish-fed fish meal	[31]
<i>S. cerevisiae</i>	Commercial strain	250 g ton ⁻¹ , 30 days	Nile tilapia, 50 ± 5 g	↑ growth performance, white blood cell counts and histopathology	[32]
<i>S. cerevisiae</i>	Commercial strain	4, 6 or 8 g kg ⁻¹ , 30 days	Pirarucu, 9.8 ± 1.4 g	↑ growth performance ↓ cholesterol	[33]
<i>S. cerevisiae</i>	Commercial strain, Idun industry, Norway	300 g kg ⁻¹ , 21 days	Atlantic salmon, 114 g	↑ nutrient digestibility and immune responses	[34]
<i>S. cerevisiae</i>	NI	0, 1, 2 or 4 g kg ⁻¹ , 90 days	Rohu, 5.69 ± 0.02 g	↑ growth performance, feed utilization and hematobiochemical indices Variations in intestinal microbiota (total viable and LAB counts) and intestinal morphology	[35]
<i>S. cerevisiae</i>	NI	0, 1, 2 (SC2) or 4 (SC4) g kg ⁻¹ , 16 weeks	Sea bream, 31.23 ± 1.2 g	↑ growth performance parameters via SC2 and SC4 feeding and intestinal morphology SC4 feeding boosted innate immune response	[36]
<i>S. cerevisiae</i> fermentation product (DVAQUA)	Commercial fermentation product	0.5 g kg ⁻¹ , 16 weeks	Hybrid tilapia, ~47 g	↑ non-specific immunity and increased intestinal bacterial count and bacterial diversity	[37]
Lyophilized whole yeast, <i>S. cerevisiae</i>	Commercial strain	1, 5 or 10 g kg ⁻¹ , 4 weeks	Gilthead seabream, 166 ± 16 g	↑ phagocytic activity, respiratory burst activity, complement activity and myeloperoxidase activity	[38]
<i>S. cerevisiae</i> , nucleotides	NI	0.5, 1.5, and 2.5 g kg ⁻¹ , 30 days	Nile tilapia, 42.9 ± 0.14 g	↑ blood proteins, leukocytes, antioxidant activity, non-specific immunity, cytokine gene expression and disease resistance against <i>Aeromonas sobria</i>	[39]
<i>S. cerevisiae</i> , nucleotides	NI	500 mg kg ⁻¹ , 80 days	European sea bass, 14.33 ± 0.18 g	↑ growth performance, lipid efficiency and anti-inflammatory TGF-β Promoted beneficial lactic acid bacteria <i>Weissella</i> and <i>Leuconostoc</i>	[40]

Table 1. Cont.

Species	Isolated from	Doses and Duration	Finfish Species Investigated	Parameters Investigated	References
<i>S. cerevisiae</i> -originated free nucleotides	Commercial product	170, 320 or 470 ppm, 60 days	Nile tilapia, ~7.8 g	↑ complement hemolytic activity Serum lysozyme concentration, intestinal villi height and density and survival toward <i>A. hydrophila</i> via N470 feeding → growth performance	[41]
<i>S. cerevisiae</i> , hydrolysate	Commercial hydrolysate (Sintun Aquatic Technology Co., Ltd.)	0.1 and 0.2%, 8 weeks	Large mouth bass, 34 g	→ growth performance, hepatosomic index and organ coefficient Modulation of gut microbiota ↓ Fusobacteria, Cyanobacteria, Tenericutes and Actinobacteria via 0.2% inclusion	[42]
<i>Debaryomyces hansenii</i> 97	Fish intestine	5×10^6 CFU mL ⁻¹ , 3 days	Zebrafish larvae	↑ survival against <i>Vibrio anguillarum</i> and the modulation of gut microbiota and metabolic pathways	[43]
<i>D. hansenii</i>	NI	1.1% of <i>D. hansenii</i> (1.7×10^6 CFU), 70 days	Gilthead seabream	↑ of somatic growth and improvement in feed conversion Modulation of gut microbiota, characterized by reduction in abundances of several Proteobacteria, especially opportunistic bacteria	[44]
<i>Geotrichum candidum</i>	Fermented milk	10^9 CFU L ⁻¹ , 70 days	Rohu larvae	↑ growth performance, protease, amylase and cellulase activities and survival after <i>Staphylococcus aureus</i> challenge	[45]
<i>Geotrichum candidum</i> QAUGC01	Commercial dairy product yogurt	10^9 CFU g ⁻¹ , un-encapsulated and encapsulated, 11 weeks	Rohu, 20 ± 2.34 g	↑ growth rate, protease, amylase, cellulase, RBCs, Hb, HCT, WBCs, MCHC, respiratory bursts and phagocytic activity, total protein, lysozyme and IgM Upregulation of heat shock protein 70 gene in muscle, intestine and liver ↓ serum AST and ALT activities, total cholesterol and triglyceride Encapsulated diet revealed best results	[46]
	Local fermented milk product of curd	10^9 CFU g ⁻¹ , 90 days	Rohu fingerings	↑ growth performance, hematological profile and digestive enzymes Modulated the gut microbiota	[47]

Table 1. Cont.

Species	Isolated from	Doses and Duration	Finfish Species Investigated	Parameters Investigated	References
	Grapes from Hubei Center for Industrial Culture Collection and Research	C: 0, T1:10 ⁶ , T2:10 ⁷ , T3:10 ⁸ , T4:10 ⁹ , T5:10 ¹⁰ , T6:10 ¹¹ , CFU kg ⁻¹ , 60 days	Gibel carp	↑ feed utilization; α-amylase activity immunity; expression of immune related genes; <i>il-1β</i> , <i>tnf-α</i> , <i>hsp70</i> and <i>tlr-2</i> in liver; and disease resistance against <i>Aeromonas hydrophila</i> Modulation of the gut microbiota	[48]
<i>Sporidiobolus pararoseus</i>	By-product of the biodiesel production process	T1 (control), T2 (5), T3 (10), and T4 (20) g kg ⁻¹ , 90 days	Nile tilapia	↑ growth performance (T3 and T4 diets). All treatments improved immune response and disease response against <i>S. agalactiae</i> .	[49]
<i>Cyberlindnera jadinii</i>	NI	10% inclusion, 42 days	Atlantic salmon, 136 ± 0.25g	↓ inflammation and enterocyte histology	[50]
Torula yeast (<i>Cyberlindnera jadinii</i>)	Commercial product, Arbiom Inc. (Durham, NC, USA)	Inclusion level (0, 10 and 20%), 35 days	Atlantic salmon, 1.14 g	→ growth performance (20% inclusion) Modulated the gut microbiota (decreasing <i>Tepidmicrobium</i> and <i>Lactobacillus</i> , but a slight increase in <i>Weisella</i> was noted with increasing torula levels)	[51]
<i>Yarrowia lipolytica</i>	Fish intestine	5 × 10 ⁶ mL ⁻¹ , 3 days	Zebrafish larvae	↑ survival against <i>V. anguillarum</i> and the modulation of the gut microbiota and metabolic pathways	[43]
<i>Aspergillus oryzae</i>	No further information was given, Bio'c company, Uchida, Japan	1 g kg ⁻¹ , 60 days	Nile tilapia	↑ growth performance, antioxidative enzymes, GPX and immunity Modulation of hematocrit, hemoglobin, red blood cells, white blood cells, total protein, and digestive enzymes	[11]
<i>Aspergillus niger</i>	Laboratory strain, no further information was given	0, 10 ³ , 10 ⁶ CFU g ⁻¹ , 60 days	Common carp	↑ Growth performance, protein efficiency ratio and lipid efficiency ratio, plasma levels of lysozyme and total immunoglobulin, red blood cell counts, haemoglobin concentrations, mean corpuscular haemoglobin, mean corpuscular volume values and lymphocyte counts	[12]
<i>Streptomyces</i> sp.	Catlintestine	Dose not given, 15 days	Swordtail, 0.4 g	↑ growth and food conversion	[52]
<i>Streptomyces</i> sp.	Sediment	Dose not specified, 15 days	Common platy, 0.4 g.	↑ food conversion rate, food conversion efficiency and growth	[53]

Table 1. Cont.

Species	Isolated from	Doses and Duration	Finfish Species Investigated	Parameters Investigated	References
<i>Streptomyces chartreusis</i>	Soil ecosystem	Control (0), 10 ⁵ (S1), 10 ⁶ (S2), and 10 ⁷ (S3) CFU g ⁻¹ , 2 months	Common carp, ~14 g	↑ growth performance parameters, regardless of inclusion levels Different doses of <i>S. chartreusis</i> increased serum total Ig and lysozyme activity compared to those fed the control diet → serum antioxidant enzyme activity (CAT, SOD and GPx)	[54]
<i>Streptomyces griseus</i>	Field sites	Exposed to 10 ² –10 ⁶ spores mL ⁻¹ for up to 96 h.	Fish gill pathology, with bream and rainbow trout being more sensitive than carp, trench and roach	Elicits pathological changes to the gills These changes include hyperplasia, leading to the fusion of the secondary lamellae and loss of microridging on the filament epithelium of the primary lamellae	[55]
Anisomycin (Ani), a metabolite produced by <i>Streptomyces griseolus</i>	NI	Dose NI, 7 days	Zebrafish, 3.20 ± 0.15 cm	Ani showed strong anti-SVCV activity in vivo, as indicated by inhibiting viral gene expression and the increased survival of zebrafish	[56]
<i>Streptomyces fradiae</i> and <i>Streptomyces</i> sp.	Marine sponges, <i>Callyspongia diffusa</i> , <i>Mycale mytilorum</i> , <i>Tedaniaanhelans</i> and <i>Dysidea fragilis</i>	Dose NI, 50 days	Swordtail, ~0.6 g	↑ growth	[57]

NI—no information given. ↑—increase; → no effect; ↓—decrease. Rainbow trout (*Salmo gairdneri*); catla (*Catla catla*); European sea bass (*Dicentrarchus labrax*); swordtail (*Xiphophorus hellerii*); common platy (*Xiphophorus maculatus*); hybrid tilapia (*Oreochromis niloticus* ♀ × *O. aureus* ♂); Egyptian African catfish (*Clarias gariepinus*); Nile tilapia (*Oreochromis niloticus*); pirarucu (*Arapaima gigas*); Atlantic salmon (*Salmo salar*); gilthead seabream (*Sparus aurata*); zebrafish (*Danio rerio*).

2.1. *Saccharomyces*

Saccharomyces cerevisiae, known as baker's yeast, is a unicellular and well-established model system for understanding fundamental cellular processes relevant to higher eukaryotic organisms [58]. The species is commonly used in fermentation and has been instrumental in winemaking, baking and/or brewing since ancient times. *S. cerevisiae* was the first eukaryotic organism whose genome was sequenced. As it is easy to grow and genetically manipulate, it has always been at the forefront of biotechnological advances. Although yeast cells are primarily reported on ripe fruits, *Saccharomyces* and some other yeast genera are reported in the GI tracts of finfish [7,59–61]. Most published studies involving yeasts as probiotics have demonstrated the beneficial effects of dietary-administered *S. cerevisiae* in fish. Studies involving *S. cerevisiae* and its cellular components (β -glucan, oligosaccharides, enzymes) could improve growth and physiological activities in fish or other aquatic organisms, suggesting their prospective applications as functional feed additives like probiotics, prebiotics, synbiotics, postbiotics and parabiotics/paraprobiotics [62]. The administration of *Saccharomyces* is commonly carried out in aquaculture [10], and to avoid overlaps, only the studies discussed in this review are presented in Table 1.

Noh et al. [63] studied the effect of supplementing *S. cerevisiae* with *Streptococcus faecium* in the diet of Israeli carp (*Cyprinus carpio nudus*). They revealed improved growth response and nutrient utilization in fish fed probiotic-supplemented diets vs. diets without probiotic supplementation. Later, Lara-Flores et al. [64] evaluated a probiotic mix consisting of *S. faecium*, *Lactobacillus acidophilus* and *S. cerevisiae* as growth promoters in Nile tilapia (*Oreochromis niloticus*) fry and revealed that diet supplemented with *S. cerevisiae* improved growth performance and feed efficiency, suggesting that yeast might be considered to be an appropriate growth-stimulating additive in tilapia cultivation. Subsequently, *S. cerevisiae* has been reported to enhance growth performance, immune responses and disease resistance in various finfish, such as rainbow trout (*Oncorhynchus mykiss*), [27] common carp (*Cyprinus carpio*) [65], grouper (*Epinephelus coioides*) [66], Nile tilapia [67], olive flounder (*Paralichthys olivaceus*) [68], and hybrid striped bass (*Morone chrysops* × *M. saxatilis*) [69–71], as well as and in carp culture [72,73].

Yeasts have been found to show protective effects against a broad range of pathogens, including parasites, bacteria and viruses. Grouper fed a diet containing *S. cerevisiae* P13 isolated from fermented peaches revealed significantly higher survival rates than the control diet after challenges with *Streptococcus* sp. and an iridovirus, respectively [66]. A significant increase in lysozyme activity ($p < 0.05$) was observed in Nile tilapia fed diets containing *S. cerevisiae* at 10 g kg^{-1} (Biosal[®], KW Alternative Feeds, Leeds, UK) for 21 days [74]. Feeding with *Lactobacillus plantarum*, *L. acidophilus* and *S. cerevisiae* in combination improved growth, feed efficiency, blood biochemistry, survival rate and non-specific immune responses in ciliate parasite (*Uronema marinum*)-infected olive flounder [68]. The study revealed enhanced superoxide anion production and increased serum aspartate aminotransferase and alanine aminotransferase levels when fed the *S. cerevisiae*-supplemented diet. A diet supplemented with *S. cerevisiae* treated with β -mercaptoethanol improved the immune response and growth of juvenile rainbow trout challenged with *Yersinia ruckeri* more effectively than whole-cell yeast and n-3 highly unsaturated fatty acid (HUFA)-enriched yeast [75]. Similarly, channel catfish (*Ictalurus punctatus*) juveniles fed diets supplemented with whole cells of *S. cerevisiae* (Levucell SB20[®]) or yeast sub-components, e.g., commercial preparations of β -glucan (MacroGard[®] and Betagard-A[®]) revealed significantly higher survival rates after being challenged with *Edwardsiella ictaluri* than catfish fed the controlled diet [76]. The inclusion of dietary β -glucan (0.5–1.0%) produced from *S. cerevisiae* was efficient at improving thermal tolerance, immunity, and disease resistance in golden mahseer (*Tor putitora*) fry [77].

The inclusion of baker's yeast in the feed was reported to improve the growth rates of Nile tilapia [67], rohu (*Labeo rohita*) [78] and African sharp-tooth catfish (*Clarias gariepinus*) [79]. Further, live baker's yeast supplementation increased carcass protein deposition in Nile tilapia and improved protection against *Aeromonas hydrophila* [67,80]. Pooramini et al. [81] reported the positive effects of *S. cerevisiae* on growth parameters, survival and carcass quality in rainbow trout fry. While evaluating the interactive effects of dietary protein (35% or 45% crude protein) and yeast levels (0.0, 0.50, 1.0, 2.0, or 5.0 kg^{-1} diet) for Nile tilapia fry and their challenge with *A. hydrophila*, $2.0 \text{ g yeast kg}^{-1}$ diet with 45% CP was determined to be the most suitable for maximum growth and resistance against *A. hydrophila* infection [82]. However, at higher inclusion levels, 20, 30 and 40% of *S. cerevisiae* resulted in a decrease in growth performance and nutrient utilization efficiency in Nile tilapia [83]. In a study of rainbow trout fry fed 0, 1, 5 and 10% yeast supplements, a decline in growth performance with supplementation at 10% was recorded in the rainbow trout fry [84]. Further, the study noticed decreased protein and increased ash content in the carcasses with increased yeast supplementation. However, the dietary administration of *S. cerevisiae* var. *elipsoidous* enhanced the resistance against salinity stress in rainbow trout fry. Although the specific reasons for the poor performance associated with higher inclusion levels are not properly discussed, the overstimulation of the immune system and consequent misuse of resources may give an explanation.

Caruffo et al. [85] evaluated the probiotic properties of 15 yeast strains (isolated from the gut of diverse fish species) for the protection of zebrafish (*Danio rerio*) larvae following a *Vibrio anguillarum* challenge. The results indicated that 13 yeast strains, including a strain of *S. cerevisiae* (Sc86) isolated from yellowtail (*Seriola lalandi*), significantly increased survival rates with regard to *V. anguillarum*. Mohammadi et al. [26] evaluated the dietary inclusion of *S. cerevisiae* (0, 0.5%, 1% and 2% levels) and recorded a significantly improved growth performance of convict cichlid (*Amatitlania nigrofasciata*) at a 2% inclusion level, but no significant difference was detected in whole-body protein content. However, an inclusion level of 2% *S. cerevisiae* significantly improved growth, as did an increase in the carcass protein content in three-spot cichlids (*Cichlasoma trimaculatum*) [86], while the supplementation of *S. cerevisiae* at a 3 g kg⁻¹ feed improved the growth performance and feed utilization of Java barb (*Barbonymus gonionotus*) fingerlings [87].

A yeast-based commercial probiotic (Aqualase[®]) consisting of *S. cerevisiae* and *Saccharomyces elipsoedae* improved growth, as well as the modulation of immunity and intestinal microbiota in rainbow trout [21]. The study revealed an increase in intestinal LAB population, elevated lysozyme activity, and the pathogen inhibitory potential of skin mucus in all yeast-fed groups. Moreover, serum lysozyme activity, IgM levels, and the respiratory burst activity of blood leukocytes were elevated, suggesting that the dietary administration of yeasts influenced humoral and cellular immune parameters. An improvement in intestinal microbiota following the addition of *S. cerevisiae* in the diet (0.6%) was also reported for GIFT tilapia (*Oreochromis mossambicus*) [88]. However, analyses of the gut bacterial community were carried out via the culture-dependent method, followed by physiological and biochemical characterization. Previously lyophilized *S. cerevisiae* was found to enhance cellular innate immune response, e.g., myeloperoxidase, phagocytic, respiratory burst, and cytotoxic activities, of head-kidney leucocytes in gilthead seabream (*Sparus aurata*); however, the humoral response was not influenced [38]. Such immunomodulatory features could be linked to the cellular components of yeasts, principally the β -glucan, which is one of the most well-documented immune stimulants in fish [89]. In addition, yeasts' nucleic acids and mannan oligosaccharides may be associated with immune-stimulatory effects [38]. Accordingly, Li et al. [90] revealed that dietary supplementation of an oligonucleotide product (Ascogen P) prepared from brewer's yeast positively influenced the immune responses to and resistance of juvenile hybrid striped bass against *S. iniae* infection. Abu-Elala et al. [91] evaluated the role of dietary *S. cerevisiae* as a probiotic (BGY-35[®]), its extract as a prebiotic (mannan-oligosaccharide, Bio-MOS[®]) and the mixture of BGY-35[®] and Bio-MOS[®] in Nile tilapia. Significant improvement in growth performance and the activation of non-specific cellular, as well as humoral immunological, responses were recorded. Furthermore, increased resistances in probiotic-, prebiotic- and synbiotic fed fish challenged with the pathogenic strains of *A. hydrophila*, *P. fluorescens* and *Flavobacterium columnare* were displayed. Based on their results, the authors suggested using *S. cerevisiae* in synbiotic form as functional feed additives for Nile tilapia. Furthermore, the groups administrated with *S. cerevisiae* noticed the colonization of yeast cells in conjunction with the increased length and density of the intestinal villi, facilitating the digestion and absorption of food. Similar results were previously reported by Gatesoupe [7], showing that the intestinal colonization of *S. Cerevisiae* accelerates the maturation of the digestive system in fish fry, while growth and metabolism were revealed in older fish.

Investigating the importance of viable yeast cells and their secretory metabolites, Ran et al. [29] indicated the advantages of using live yeast as a dietary supplement for Nile tilapia, as evidenced by the improved gut microvilli morphology, reduced *hsp70* expression level and reduced intestinal inflammation, suggesting the beneficial role of yeast secretory metabolites. However, secretory metabolites might not play a significant role in growth promotion and disease resistance, as both live and inactivated yeast provide protection against *A. hydrophila* infection. In contradiction to other reports [21,88], yeast supplementation did not significantly influence the diversity of the autochthonous microbiota evaluated via 16S rRNA gene pyrosequencing and gut microbiome analysis [29]. In another study, the

supplementation of *S. boulardii* in diets was revealed to stimulate the growth, feed efficiency and survival rates of common carp fingerlings [92]. Rotifers are important zooplankton that supply trace minerals for finfish larvae in commercial hatcheries. Nematzadeh et al. [93] revealed that using rotifer (*Brachionus plicatilis*) grown with zinc-enriched *S. cerevisiae* improved the growth, reproduction and body composition of the rotifer culture. The dietary supplementation of *S. cerevisiae* enhanced innate immunity, lowered pathogenic bacteria load in fish muscle and modulated the gut microbiota in Nile tilapia reared in low-input ponds, demonstrating that *S. cerevisiae* was more effective as a probiotic compared to *Bacillus subtilis* [94,95]. The administration of commercially produced *S. cerevisiae* as a feed additive improved growth, feed utilization and resistance against *P. fluorescens* in freshwater catfish (*Mystus cavasius*) [96].

Hansen et al. [44] adopted the laboratory-scale downstream processing of *S. cerevisiae* through direct inactivation via spray-drying, autolysis and cell crushing. The post biotics produced via down-stream processing were evaluated for their nutritional value and health effects in the diets of Atlantic salmon (*Salmo salar*), and the increased solubility of protein and β -glucan resulted in increased protein digestibility and immune stimulatory effects [44]. In a 60-day study, MajharulIslam et al. [97] reported that *S. cerevisiae* administration to Nile tilapia significantly improved growth performance, feed utilization, villus structure and the number of goblet cells present when the fish were fed a diet supplemented with 4 g kg^{-1} *S. cerevisiae*. Further, adding methionized yeast (methionine @ 50 g kg^{-1} feed) to the diet positively affected growth and nutrient utilization in the hybrid African catfish *Clarias gariepinus* \times male *Heterobranchus longifilis*. In a recent study used to evaluate the biochemical and molecular properties of four yeast cell-wall extracts from *S. cerevisiae*, Rawling et al. [98] revealed that extracts varying in structure and composition differently affected the innate mucosal tissue responses and the innate immunity of zebrafish intestine.

2.2. *Candida*

Candida belongs to the class Saccharomycetes. Past evaluations of the intestines of diverse fish species have revealed gut-associated *Candida*, such as *Candida albicans* within the GI tract of rainbow trout [99]. Further, *Candida* sp., along with some other yeast species, was described as forming a dominant part of the gut microbiota in some samples of rainbow trout [7]. Later, the tannin-degrading ability of the autochthonous *Candida tropicalis* (GU911469) and *Candida parapsilosis* (GU939630) were reported from the GI tracts of tilapia (*Oreochromis mossambicus*) and rohu, respectively [59]. The phytase-producing ability of *C. tropicalis* (JX532154) isolated from climbing perch (*Anabas testudineus*) and *C. tropicalis* (JX532155) isolated from silver carp (*Hypophthalmichthys molitrix*) were also documented [61]. The authors opined that the tannin- or phytate-degrading microbiota might provide an ecological advantage to the fish by enabling them to conquer the anti-nutritional effects of dietary tannins and phytates. Recently, Siangpro et al. [100] isolated 176 acid-tolerant yeasts from the GI tracts of diverse fish species, of which 15 yeast isolates representing antagonism against pathogenic bacteria of Nile tilapia were characterized for probiotic properties (adhesion potential, biofilm formation, and resistance to acid/bile). Among all yeast isolates, a strain of *C. Tropicalis* (LC735681) exhibited maximum antipathogenic activity, suggesting its prospective application as an alternative to antibiotics for sustainable fish farming [100]. Regardless, there is no information regarding the use of *Candida* sp. as a probiotic supplement in finfish aquaculture, but some information is available regarding the use of *Candida* in shrimp aquaculture [16].

2.3. *Cryptococcus*

Cryptococcus is often referred to as ‘the sugar yeast’ due to the thick coating of polysaccharides surrounding its cell. *Cryptococcus* is a genus within the family Cryptococcaceae. It is reported in the GI tracts of several fish species [7,47], but to our knowledge, no information is available regarding its use as a probiotic supplement in aquaculture.

2.4. *Debaryomyces*

Debaryomyces hansenii is a hemi-ascomycetous yeast commonly reported in natural substrates like soil and food, although it is also reported in the GI tract of rainbow trout [31]. The probiotic and nutritional effects of *Debaryomyces* in fish were presented in a comprehensive review by Angulo et al. [22], and to avoid overlaps, we recommend that interested readers have a closer look at the papers published before 2020 and discussed in this review, as mentioned above. In the study of Vargas et al. [43], the authors revealed that *Debaryomyces hansenii* supplemented with a zebrafish diet improved survival against *V. anguillarum*; modulated the gut microbiota; affected carbohydrate, lipid and amino acid metabolism; and prevented increase of *Ensifer* (nitrogen-fixing bacteria) and *Vogesella* (Gram-negative bacteria) unfavorable for larval survival. In another study, Sanahuja et al. [44] reported that *D. hansenii* administration in a gilthead seabream diet increased growth and improved feed conversion, modulating the gut microbiota without affecting the intestinal cell organization, even though *D. hansenii* supplementation modified the composition of lectin in the mucinous content of goblet cells. The modulation of gut microbiota was characterized by a reduction in the abundance of the genera *Anaerococcus*, *Asciidiaceihabitans*, *Hydrogenophaga* and *Variovora*. In a more recent study, *Debaryomyces nepalensis* and three other autochthonous yeast strains (viz., *Cutaneotrichosporon jirovecii*, *Blastobotrys proliferans* and *Diutina catenulata*) with potential probiotic properties were recorded from the intestine of the goldfish *Carassius auratus* [101]. The documented strains were noticed to interact with several fish-associated bacterial pathogens, namely *A. hydrophila*, *Lactococcus garvieae*, *V. anguillarum*, *Vagococcus salmoninarum* and *Yruckeri*.

2.5. *Geotrichum*

Geotrichum candidum is a filamentous fungus used in the dairy industry for cheese ripening and flavoring. Still, four recent studies have used *G. candidum* as probiotic supplements for rohu [45–47] and gibel carp [48]. Sanahuja et al. [45] showed that *G. candidum* supplemented with the rearing water of rohu larvae increased growth performance; digestive enzyme, protease, amylase and cellulase activities; and crude protein in muscle and improved the survival of larvae in response to challenge by *Staphylococcus aureus*. Ibrar et al. [46] evaluated the application of 10^9 CFU g^{-1} of un-encapsulated (free) and encapsulated *G. candidum* QAUGC01 in rohu diet through an 11-week study and revealed improved growth performance, enzyme activities (protease, amylase and cellulase) and immunity and an upregulated heat shock protein gene in rohu. However, encapsulation had the most profound effect, suggesting its application as a feed additive in practical/commercial semi-intensive earthen pond culture systems.

In the gibel carp study of Noor-Ul et al. [48] seven inclusion levels of *G. candidum* (0, 10^6 , 10^7 , 10^8 , 10^9 , 10^{10} and 10^{11} CFU) revealed that *G. candidum* displayed higher intestinal α -amylase activity, but no difference was demonstrated for lipase and trypsin activities and those of the control. Gut microbiota were modulated as the relative abundance of the phylum proteobacteria, actinobacteria, firmicutes and bacteroidetes noted in fish-fed filamentous fungi. At the same time, in control-fed fish, a higher percentage of pathogenic bacteria belonging to the order Aeromonadales and Vibrionales were displayed. After the challenge with *A. hydrophila*, significantly higher respiratory burst activity, IgM levels and aspartate transaminase, lysozyme and alanine transaminase activities were noted in fish fed 10^6 and 10^8 CFU of *G. candidum*. The expression of immune-related genes, namely *il-1 β* , *tnf- α* , *hsp70* and *tlr-2*, in the fishes' livers were significantly affected by the administration of *G. candidum* after the *A. hydrophila* challenge. This study showed that *G. candidum* could be a potential probiotic, as productive results can be achieved using the lower doses, in particular 10^6 – 10^8 CFU kg^{-1} . Ghori et al. [47] investigated the effects of *G. candidum* supplementation on rohu fingerlings and revealed improvements in the growth performance, hematological profile and amylase and cellulase activities and modulated the gut microbiota through the absence of *Staphylococcus saprophyticus* and *Sporobolomyces lactosus*, along with the relative abundances of *Trichosporon* and *Cryptococcus*.

2.6. *Leucosporidium*

Leucosporidium is a genus of psychrophilic or asporogenous yeasts and belongs to the family Leucosporidiaceae, order Leucosporidiales, which includes five species, namely *L. antarcticum*, *L. fasciculatum*, *L. fellii*, *L. golubevii* and *L. scottii* [102]. All species grew well at subzero temperatures ($-1\text{ }^{\circ}\text{C}$) to the maximum temperature of $18\text{--}20\text{ }^{\circ}\text{C}$, with glucose being the substrate [103]. Although *Leucosporidium* sp. is frequently reported in rainbow trout intestine, information regarding fish gut-associated *Leucosporidium* from other fish species is scant [104].

The physiological properties and enzymatic potential of the strains under this genus suggest their likely application for low-temperature and marine water aqua-farming. For example, *L. scottii* is the only species able to grow richly on marine substrates at mesic temperatures [105] with a heterobasidiomycetous life cycle that is morphologically ascomycetous in nature; like *Saccharomyces cerevisiae*. *L. antarcticum* is a widespread, endemic Antarctic marine yeast found in cold marine waters, and it was reported to be used to produce intracellular β -fructofuranosidase, as well as intra- and extracellular glucosidases [106]. A novel extracellular subtilase was reported by *L. antarcticum* isolated from water from Admiralty Bay [107]. In addition, *Leucosporidium* spp. was found to produce some other enzymes, like cold-adapted extracellular serine proteinase [108], invertase, α -glucosidase [106], extracellular lipase [109], amylase laccase, pectinases [110] and β -fructofuranosidase [111]. The effects of live yeast and/or the incorporation of exogenous enzymes into diets to improve fish growth and digestive enzyme activity were discussed in previous studies [7,112–114].

2.7. *Pichia*

Pichia is a genus of yeasts in the family *Pichiaceae* with spherical, elliptical, hat-shaped, hemispherical or round ascospores and oblong acuminate cells. The methylotrophic yeast *Pichia pastoris* utilizes glucose, glycerol and methanol as a carbon and energy source and is widely used in the biochemical research and biotech industries to manufacture enzymes and pharmaceuticals [115,116]. Since yeast has generally been recognized as safe (GRAS) by the US Food and Drug Administration (FDA), *Pichia* has been cultivated on a commercial scale and sold directly as protein-containing animal feed [117]. In addition, it can utilize a wide range of sources of nitrogen and phosphorus, making it a potential factor in reducing environmental pollution caused by organic wastes from agriculture [118].

Fish gut-associated *Pichia* spp. and their probiotic attributes were indicated in some previous reports. The tannase-producing ability of *P. kudriavzevii* (GU939629) was identified in the GI tract of common carp [59]. In another study, *P. kudriavzevii* (KT582009) isolated from the gut of Nile tilapia displayed an ability to produce diverse exo-enzymes and antagonism against fish pathogenic *A. hydrophila* [119]. Acosta et al. [120] demonstrated that the immersion of fish into the growth hormone (GH)-rich recombinant *Pichia pastoris* preparation could be the most efficient and convenient method for GH administration to promote growth in tilapia. The recombinant *P. pastoris* strain could synthesize mature peptide of crucian carp (*Carassius auratus*) c-type lysozyme with antibacterial activity and good stability [121]. The dietary application of non-modified *P. pastoris* at 10^9 CFU g^{-1} of feed did not improve the growth performance of jundiá (*Rhamdia quelen*) larvae, as growth performance was similar to that of the control diet [122]. More recently, the application of the plant endophytic yeasts *Pichia fermentans* and *Meyerozyma caribbica* significantly improved the growth, nutrient composition, minerals, hematological parameters, length of intestinal villi and kidney function of the carp *Barbonymus gonionotus* [123], and *P. fermentans* at 0.94×10^8 CFU kg^{-1} feed gave the maximum positive effects of *B. gonionotus*, indicating its probiotic potential for aquaculture applications. The bioprocessing of oil-cake [124] and aquatic weed [125] through solid-state fermentation (SSF) by the tannase-producing yeast *P. kudriavzevii* (GU939629) was identified as an effective strategy for the deactivation of anti-nutritional factors and value addition of the plant feedstuffs for their likely utilization in formulated fish feed.

Sealey et al. [126] reported that diets supplemented with *P. guilliermondii* at 0.3% or 0.6% for juvenile rainbow trout improved growth, food conversion efficiency, feed intake, protein retention efficiency and disease resistance against *Yersinia ruckeri* and *Flavobacterium psychrophilum* through a 16-week study in a recirculating aquaculture system. No effect of *Pichia* supplementation on mortality was observed. Further, the cell-surface phytase of *P. pastoris* was highlighted as being a potential feed supplement [127]. *P. fermentans* improved the growth, hematological–biochemical composition, and morphology of internal organs in *Barbonymus gonionotus* [123]. *P. kudriavzevii* had the ability to produce phytase that could, ideally, be useful in the feed and animal industries [128].

2.8. *Rhodospiridium*

Rhodospiridium is a type of red basidiomycete that accumulates carotenoids, neutral lipids and enzymes relevant to the chemical and pharmaceutical industries. They metabolize all major components of lignocellulosic biomass (cellulose, hemicellulose and lignin) and are potential hosts for metabolic engineering to produce terpenes and fatty acids. In fish, a strain of *Rhodospiridium babjevae* was only isolated from the reared croaker (*Cilus gilberti*) intestine, whereas *Rhodospiridium sphaerocarpum* was only isolated from wild croaker intestine [129]. Both *R. babjevae* and *R. sphaerocarpum* have previously been identified in marine environments, which also can explain their presence in the fish gut [130,131]. *Rhodospiridium* spp., as a carotenoid-rich red yeast, has been reported to accumulate intracellular lipids as high as 60% of its cell dry weight using glucose as the carbon source [132]. It has been successfully used as a dietary supplement in aquaculture to reduce oxidative stress in aquatic animals [133].

2.9. *Rhodotorula*

Rhodotorula spp. belong to the phylum ‘Basidiomycota’, family ‘Cryptococcaceae’, class ‘Microbotryomycetes’, and order ‘Sporidiobolales’, which are pigmented basidiomyceteous yeasts (fungi) commonly reported in different unfavorable ecosystems, as well as in fish [31]. Biomass of *Rhodotorula glutinis* strains could be used as the natural sources of α -L-arabinofuranosidase, lipases, invertase, pectinases, invertase and tannin acyl hydrolase, particularly phenylalanine ammonia lyase (PAL) [134,135]. More importantly, carotenoids, lipids and industrial enzymes synthesized by *R. glutinis* strains have advantages, mainly due to their higher biotransformation rates independent of climate and low costs [136,137]. *Rhodotorula* can metabolize avidly short-chain fatty acids, such as acetic, propionic and butyric acids, essential for the gut epithelium and other physiological functions [138,139]. *Rhodotorula* spp. secrete various enzymes, such as xylanase, cellulase and amylase [140], contributing to the degradation of the viscosity-generating soluble fibers in foods, and they are considered nutritionally advantageous [141]. *Rhodotorula* protease has been reported to degrade bacterial toxins [142]. Furthermore, *Rhodotorula* produces folates, lipids, carotenoids and proteins that are essential nutrients for all living organisms [141,143,144]. Dietary *Rhodotorula* supplementation “as an alternative to antibiotics” improved growth and disease resistance in juvenile Japanese spiky sea cucumbers [145].

Rhodotorula supplementation was reported in juvenile Nile tilapia (*Oreochromis niloticus*) to improve growth performance, antioxidant capacity, histomorphology and immune responses [146]. Dietary *R. mucilaginoso* enhanced the growth performance, immune responses and disease resistance of the juvenile golden pompano *Trachinotus ovatus* [147]. Carotenogenic *Rhodotorula paludigena* VA 242 served as a pigment-enhancing feed additive for the ornamental fish koi carp, and improved growth and survival rates were also recorded [148]. Feed supplements with a *Rhodotorula* cell mass have been proven safe and non-toxic in animals [149–151]. The dietary supplementation of *Rhodotorula* sp. C11 at 10^5 and 10^6 CFU g^{-1} improved growth and resistance against *Vibrio splendidus* infection in juvenile sea cucumber (*Apostichopus japonicas*) [145]. Pacific white shrimp fed dietary yeast (*Rhodotorula* sp.) enhanced intestinal health, growth, disease resistance and immune responses [152,153]. Yeasts are often applied to aquaculture as live probiotics or

feed ingredients [154]. Dietary hydrolyzed *R. mucilaginosa* can influence intestinal health, immune response, and the ammonia resistance in Pacific white shrimp (*Litopenaeus vannamei*) [155]. Red yeast has excellent industrial potential and has piqued the interest of the food, pharmaceutical, cosmetics and feed industries [156]. Microbial carotenoids have received scholarly attention [157], and Maldonado et al. [158] reported that a maximum of 745 $\mu\text{g L}^{-1}$ carotenoid can be produced by *R. mucilaginosa*. *R. mucilaginosa*, which is one of the most promising pigment-producing yeasts, can be fermented using cheap industrial by-products and wastes as nutrient sources [159–161].

2.10. *Sporidiobolus pararoseus*

The red yeast *Sporidiobolus pararoseus* is a single-cell microorganism in the class Basidiomycota. In a recent study, Srinual et al. [162] suggested that red yeast (*S. pararoseus*) supplementation effectively alleviated the toxicity induced by mycotoxins and could be applied as a novel feed additive in the broiler industry. In aquaculture, mycotoxin-related issues are increasing, and in this regard, it is of interest to note that Van Doan et al. [49] investigated the effects of red yeast, a by-product of the biodiesel production process, on the growth, immunity and resistance of Nile tilapia with regard to *Streptococcus agalactiae*. Fish were fed four different concentrations of dried red yeast, namely T1 (control; T1), T2 (5), T3 (10), and T4 (20) g kg^{-1} diets for 90 days, and the results revealed the significantly improved growth performance of fish fed with the T3 and T4 compared to the control. A significant increase was observed in total carotenoid content, liver superoxide dismutase activity, serum lysozyme and albumin and disease resistance against *S. agalactiae* in fish fed with red yeast. The highest bactericidal activity was revealed in the T4 group, but no significant differences were displayed in hematology, blood chemical, malondialdehyde, body chemical composition, organosomatic indices and myeloperoxidase in all treatment groups. Based on their results, the authors concluded that the T4 diet was most promising and could be used to supplement Nile tilapia. Owing to mycotoxin-binding capacity, *S. pararoseus* has been recognized as a potential feed additive for animals [163].

2.11. *Sporobolomyces*

Anamorphic basidiomycetous yeasts of the *Sporobolomyces* taxa are known for their bright red, orange or pink appearances and belong to the order ‘Sporidiobolales’. The main carotenoids produced by the *Sporobolomyces* yeasts are β -carotene, torulene and torularhodin [164,165]. Some strains of *Sporobolomyces* yeasts can degrade patuline, a mycotoxin with mutagenic, genotoxic, immunotoxic, teratogenic and cytotoxic properties [166]. *Sporobolomyces* spp. has shown a potential application in shrimp aquaculture [167–169].

2.12. *Trichosporon*

Trichosporon belongs to the phylum ‘Basidiomycota’, class ‘Hymenomycetes’ and order ‘Trichosporonales’. Industrial interest has focused on the ability of the *Trichosporon* species to utilize a wide range of substrates, particularly aromatic compounds, aliphatic lipids, amines and complex nitrogenous compounds, as its sole sources of carbon and energy, including uric acid, ethylamine, hydroxyproline, tyramine and l-phenylamine [170]. *Trichosporon* cells or enzymes might metabolize pollutants and xenobiotics in bioremediation processes [171–173]. Furthermore, *Trichosporon asahii* strains were reported to produce lipase [174], aspartic-type peptidase [175] and antioxidant molecules [176], which could have critical applications in animal farming systems, including aquaculture. *Trichosporon cutaneum* is commonly reported in the intestines of fish and known to accelerate the development of the digestive system of fish [7]. Previous studies revealed that *T. asahii* has antioxidant enzymatic activities [176,177].

2.13. *Yarrowia lipolytica*

Yarrowia lipolytica is one of the “non-conventional” yeast species capable of synthesizing a broad group of valuable metabolites, in particular lipases and other hydrolytic enzymes, microbial oil, citric acid, erythritol and γ -decalactone. In a recent study, Vargas et al. [43] revealed that *Y. lipolytica* supplemented with a zebrafish diet improved survival against *V. anguillarum*; modulated the gut microbiota; affected the carbohydrate, lipid and amino acid metabolism; and prevented the increase in *Ensifer* and *Vogesella*.

3. Mold (*Aspergillus* spp.) as Probiotics

Apart from the production of digestive/degradation enzymes, some of the well-recognized functions of *Aspergillus* are the synthesis of antibacterial substances, the reduction in blood cholesterol levels, the inhibition of bacterial infections, the modulation of immunity and the reconstruction of the gut microbiota [178]. Further, the potential effects of *Aspergillus* on the mitigation of hypoxia and salinity stress in fish have been indicated [18,179]. Most studies on fish associated with *Aspergillus* spp. were directed towards the pathophysiological effects of the fungi in numerous fish species [180,181]. Although some molds can produce mycotoxins [182], *Aspergillus niger* and *Aspergillus oryzae* are reported to be the predominant species under the genus *Aspergillus*, conferring health benefits to aquatic animals.

3.1. *Aspergillus niger*

A. niger is the most common fungi of the genus *Aspergillus* that can be easily cultivated in laboratory conditions. Diverse strains of *A. niger* are sources of several enzymes (proteases, α -amylase, cellulase, xylanase, phytase and tannase) and bioactive compounds (citric acid, gluconic acid and itaconic acid); therefore, they are extensively used in the poultry industry [183]. However, reports on the application of *A. niger* in fish are scant. The dietary supplementation of autochthonous *A. niger*, along with *S. cerevisiae* (6×10^6 cells g^{-1}), improved the growth, survivability, immune parameters and ammonia excretion in the juvenile beluga sturgeon *Huso huso* [184].

In a recent study of common carp, diets containing *A. niger* (10^3 , T1 and 10^6 , T2) were fed for 60 days [12]. The authors revealed significantly improved effects on growth performance, plasma levels of lysozyme, total immunoglobulin, red blood cell counts, hemoglobin concentrations, mean corpuscular hemoglobin, mean corpuscular volume and lymphocyte counts via the administration of both T1 and T2. The activities of the digestive enzymes (protease, trypsin, amylase, lipase and alkaline phosphatase) and apparent digestibility parameters were significantly improved via the supplementation of 10^6 of *A. niger* into the diet (T2). White blood cells, hematocrit values and a number of neutrophils were also higher in treatment T2. Very few strains of *A. niger* are known to produce ochratoxin A [185]. Thus, the screening of the *A. niger* strains intended for use in probiotics applications should be conducted with the utmost care.

3.2. *Aspergillus oryzae*

The supplemental effects of dietary *A. oryzae* on fish are documented in several studies of Nile tilapia. The dietary supplementation of *A. oryzae* potentially improved the immune status and disease resistance [186], along with growth performance and intestinal histomorphometry [187], in Nile tilapia. Dawood et al. [188] conducted a 60-day feeding trial with Nile tilapia to determine the effect of dietary *A. oryzae* (at 10^6 and 10^8 CFU g^{-1} levels). They showed a significant increase in the growth performance and modulation of blood hematocrit, hemoglobin, red blood cells, white blood cells, total protein and digestive enzymes, villi length and the activity of antioxidative enzymes. However, decreased blood triglyceride and the oxidative enzyme (MDA) were reported in the *A. oryzae* group. Supplementation enhanced nitro blue tetrazolium (NBT), IgM, lysozyme, bactericidal and phagocytosis, indicating the improved immunity of tilapia. Further, the fish were subjected

to a hypoxia challenge, and the addition of *A. oryzae* to diets significantly improved the defense against hypoxia stress in Nile tilapia.

In addition, the combined application of *A. oryzae* and β -glucan as synbiotics significantly ($p < 0.05$) improved the growth, feed efficiency, hematological parameters, digestive enzymes, immunity (NBT, IgM, lysozyme, bactericidal and phagocytosis) and antioxidative capacity of Nile tilapia [11]. Fermented *A. oryzae* could enhance the growth and hematological parameters of common carp [189]. In another study, Nile tilapia juveniles were fed diets supplemented with *A. oryzae* (1 g kg^{-1} diet) for 12 weeks, and after that, they were exposed to different salinity levels for 15 days [18]. Significant increases ($p < 0.05$) in blood protein levels (albumin, globulin and total protein), non-specific immune responses (lysozyme and phagocytic activities) and antioxidant enzymes (glutathione peroxidase, catalase and superoxide dismutase), along with a significant decrease ($p < 0.05$) in the values of hemato-biochemical indices (e.g., glucose, cortisol, alanine transaminase, aspartate transaminase and malondialdehyde), were recorded. Moreover, biochemical and gene expression studies support the efficacy of dietary *A. oryzae* in alleviating salinity stress [18].

4. Actinobacteria as Probiotics

Actinobacteria are Gram-positive filamentous bacteria with high guanine and cytosine (G + C) contents in their genomes. Actinobacteria usually inhabit soil and aquatic ecosystems and are known to have significant functions in biogeochemical cycles, bioremediation and the production of bacteriocins and other potent bioactive compounds, e.g., novel enzymes and antibiotics [190]. These unique and diverse features made actinobacteria a competent candidate for use in the aquaculture industry [191]. The potent actinobacterial genera are *Streptomyces*, *Micromonospora* and a later described genus known as *Salinispora* [19], but *Streptomyces* are the most extensively studied among them.

The genus *Streptomyces* belongs to the phylum 'actinobacteria' and constitutes soil-living bacteria with a characterized branching filamentous morphology [9,192,193]. It is an excellent antibiotic producer and produces extracts that inhibit biofilm formation [194]. Members of the genus *Streptomyces* can produce different hydrolytic enzymes, e.g., amylase, protease and lipase, making them able to break down complex insoluble organic materials [195] and bacteriocin-like substances [196]. These unique physiological features of *Streptomyces* are believed to make them potential probiotics, as the secretion of exoenzymes could facilitate feed utilization and digestion in aquaculture animals once they have colonized the host intestine. Diverse strains of *Streptomyces* isolated from varied sources exhibited different probiotic properties, making them important candidates for application in the aquaculture sector. Potential probiotic attributes of *Streptomyces* include tolerance to gut conditions, antimicrobial activity against fish pathogens, inducing immune responses in fishes, growth-enhancing effects and water quality amelioration [197]. Thus, despite the production of common semi-volatile terpenoid compounds, e.g., geosmin and 2-methylisoborneol, the genus *Streptomyces* has been recognized as a prospective probiotic for aquaculture [9]. Although most studies of the probiotic application of *Streptomyces* strains in aquaculture have been conducted in shrimps [198–200], numerous studies are also available in fish, but some limitations to their use as probiotics in aquaculture are reported, producing several compounds with unpleasant odors and tastes, lateral gene transfer and biotoxicity in *Artemia salina* nauplii [193].

In a study of marine actinobacteria, the potential of *Streptomyces* strains isolated from sponges revealed the improved growth of an ornamental fish (*Xiphophorus hellerii*) [56], and the administration of *Streptomyces* as single cell protein resulted in improved growth of the ornamental fish Southern platy fish (*Xiphophorus maculatus*) [36]. The potential of *Streptomyces* as a probiotic in aquaculture was reviewed by Tan et al. [9], and to avoid overlaps, only studies published post-2016 and studies not reported in the review of Tan et al. [9] are discussed in this section. Several strains of the genus *Streptomyces* were noted to produce bioactive compounds and exhibited antagonistic activities against different fish pathogenic strains, based on which findings, their likely applications in finfish

aquaculture could be understood. Sheeja et al. [201] reported that *Streptomyces* strains isolated from the gut of marine ornamental fishes, viz. red tail butterfly (*Chaetodon collare*) and orange-lined cardinal (*Archamia fucata*), produced potential bioactive metabolites against *Vibrio cholera*. *Streptomyces ruber* EKH2 isolated from sediments of Bardawil Lake, Egypt, produced phthalate, a non-toxic bioactive dibasic acid that inhibited the fish pathogenic *A. hydrophila*, *Edwardsiella tarda*, *Pseudomonas aeruginosa* and *Vibrio ordalli* [202]. Phthalate activities were superior to commonly known standard antibiotics used in fish therapy, thus suggesting that it is a promising candidate for treating septicemic fish diseases. Marine *Streptomyces rubrolavendulae* in the form of biogranules was found to inhibit *Vibrio alginolyticus*, *V. fluviialis*, *V. harveyi* and *V. parahaemolyticus* in an in vitro co-culture experiment [199]. The extensive antibacterial activity of *Streptomyces carpaticus* MK-01 isolated from seawater collected from Daejeong, Jeju Island, was demonstrated against the Gram-positive fish pathogenic bacteria *S. iniae* and *S. parauberis* [203]. The authors recommended the use of the *S. carpaticus*-MK01 strain, as well as its antioxidant and antimicrobial compounds, as prophylactic measures in aquaculture industries.

A marine isolate (*Streptomyces* sp. S073) exhibited strong antagonism against the pathogenic *V. parahaemolyticus*. The isolate S073 could produce non-proteinaceous and thermostable siderophores that created lethal iron-limiting conditions to inhibit the pathogens [204]. Thus, the protective effects of the marine *Streptomyces* strains indicated their probiotic potential for aquaculture. A similar kind of observation was recorded with *Streptomyces* sp. SH5 isolated from marine sediment could enhance resistance against *A. hydrophila* infection in zebrafish [205]. The presence of SH5 in the rearing water strongly prevented colonization by *A. hydrophila*. Enhanced expression of the immune response genes (*tlr3*, lysozyme and *nos2a*) and reduced expression of the inflammatory genes (*il-1 β* , *il-6* and *myd88*) were recorded in zebrafish larvae, indicating the potential application of the strain to prevent pathogen infection [205]. Further, *Streptomyces* strains isolated from the gut of estuarine milkfish (*Chanos chanos*) produced antibacterial peptides that exhibited broad-spectrum antibacterial activity against *S. aureus*, *B. cereus*, *P. aeruginosa* and *E. coli* [206]. In another study, Kumaran et al. [207] recorded *Streptomyces enissocaesilis* SSASC10, a brown pigment-producing isolate that produced bioactive metabolites against fish pathogens (e.g., *Pseudomonas* sp., *V. anguillarum*, *A. hydrophila*, *V. parahaemolyticus* and *V. harveyi*), highlighting their potential use as probiotics for treating infectious fish diseases. A recent study established the probiotic potential of *Streptomyces antibioticus* EW1 (isolated from the digestive tract of earthworm *Eisenia fetida*) in juvenile catfish *Heteropneustes fossilis* [208]. In this study, *S. antibioticus* exhibited antimicrobial activity against two fish pathogens: *Aeromonas veronii* (MN602971) and *Stenotrophomonas maltophilia* (MN602972). Further, diets supplemented with *S. antibioticus* enhanced the growth, digestibility, muscle protein and survivability of *H. fossilis* [208].

5. Combined Application of Yeasts or Actinobacteria along with Other Probiotics

The probiotic organisms that are widely used in aquaculture, either as water additives or feed supplements, might include diverse strains of bacteria, bacteriophages, microalgae and yeasts [13]. It is widely accepted that the major benefits associated with applying probiotics in aquaculture are improvement in growth performance, the modulation of immunity, pathogen exclusions and disease resistance [209–211]. Regarding yeasts used as probiotics, a recent study by [212] reported that the yeasts had a high survival rate in the GI tract, an exciting finding that needs to be included and confirmed in future yeast studies. Interestingly, most of the reports available on the application of probiotics in fish or shellfish used single-strain probiotics. However, multi-strain probiotics are more effective than a single strain, as reported in a good number of studies during the last two decades [213]. Still, the evaluation of the combined administration of probiotics seemed inadequate in aquaculture compared to single-strain administration [214–216]. When compared to single-strain application, applying probiotics as multi-strain or multi-species dietary supplements could create improved benefits, as a combination of probiotics might

allow the incorporation of different mechanisms of probiotic action at once [217]. The present section primarily includes the reports in which different strains of bacteria are used in combination with yeasts/actinobacteria.

Commercial diets supplemented with *Streptococcus faecium* and a mixture of bacteria and yeast have been shown to improve growth and food conversion efficiency in catla (*Catla catla*) [218] and common carp [219]. Feeding probiotics (*L. plantarum* and *L. acidophilus*), along with *S. cerevisiae* in combination for 4–8 weeks, enhanced superoxide anion production in olive flounder [68]. The study concluded that *L. plantarum*-, *L. acidophilus*- and *S. cerevisiae*-supplemented diets might act as immunostimulants, improving the growth, feed efficiency, blood biochemistry, survival rate and non-specific immune response in *Uronema marinum*-infected olive flounder [68]. Diets supplemented with two species of bacteria (*L. lactis* and *B. subtilis*) and *S. cerevisiae* in equal proportion at a feed concentration of 10^{11} CFU kg⁻¹ improved growth and feed efficiency in rohu fingerlings, indicating that the combination of more probiotic organisms in the diet resulted in improved growth performance and nutrient utilization [214]. However, combinations of heat-inactivated probiotics in the diet failed to create positive effects, suggesting that the live probiotic microorganisms could be preferred while formulating the cost-effective nutritionally balanced carp diet [214]. In contrast, the likely application of paraprobiotics (inactivated probiotics) as a component of functional feed additives has received significant interest in recent times [62,220,221]. According to Tran et al. [221], dietary supplementation of the cell structural components as paraprobiotics can trigger anti-biofilm effects and improve growth performance, stress tolerance, immunity and defense against pathogens. Possible utilization of the yeast cells as paraprobiotics in aquaculture has very recently been indicated [62]. In an in vitro evaluation of the effects of single- and multi-strain probiotics on pathogen inhibition, Chapman et al. [222] suggested that the use of a probiotic mixture might be more effective at reducing infections and creating a combination using species with different effects against different pathogens may have a broader spectrum of action than that provided by a single strain. A synergistic effect of the probiotics' mixture containing *B. subtilis* E20, *Lac. pentosus* BD6, *S. cerevisiae* P13 and *Lac. fermentum* LW2 was recorded, depicting improved growth performance, immune response and disease resistance in Asian seabass (*Lates calcarifer*) against *Aeromonas hydrophila* [213]. In a more recent observation, the combined dietary application of probiotic yeast, *S. cerevisiae* (1%) and *L. casei* (1%) improved growth, immunity and gut health in juvenile Asian seabass [223]. The co-supplementation of *S. cerevisiae* and *L. casei* resulted in the upregulation of immune-responsive genes (*il-10* and *tnf-α*), a greater number of goblet cells in the gut mucosa and increased microvilli length. The analysis of the gut microbiome revealed decreased abundances of pathogenic *Corynebacterium* and *Staphylococcus* [223]. The combined dietary administration of *B. subtilis*, *A. oryzae* and *S. cerevisiae* improved growth, hemato-immunological parameters, innate immune response and disease resistance in Nile tilapia [186]. In contrast to the above reports, a diet with 50% *Lactobacillus* mixtures and 50% *S. cerevisiae* did not improve growth and survivability in African catfish (*Clarias gariepinus*) larvae [224].

As reports on combined applications in finfish aquaculture are limited, some pertinent facts from the shrimp and other aquatic organisms may be discussed because of their impact on the aquatic environment and productivity, apart from the benefit created for the host. The combined application of *Streptomyces* strains and *Bacillus* improved growth, immune response and resistance against *V. parahaemolyticus* in Pacific white shrimp culture, along with modulation of the water microbiota [200]. Application of the dietary hydrolyzed *R. mucilaginosa* along with *B. licheniformis* as the synbiotics could improve intestinal morphology and immune response in Pacific white shrimp more than the hydrolyzed yeast or *B. licheniformis* alone [155]. Liu et al. [225] demonstrated the effect of a commercial microbial agent (consisting of more than ten species of microorganisms, e.g., spore-forming bacteria, LAB, photosynthetic bacteria, actinomycete, etc.) in Pacific white shrimp. The study noted an increased temporal turnover rate among the bacterioplankton community in the culture water and a greater relative abundance of Rhodobacteraceae in shrimp intestine, suggesting

that the microbial mixture could accelerate bacterioplankton community turnover and shift intestinal bacterial community in aquatic organisms. However, the commercial microbial combination did not significantly improve the shrimp's growth rate or survival. Combined oral administration of *Rhodotorula* sp. H26 and *Bacillus* sp. BC26 improved digestive enzyme activity (e.g., trypsin and amylase) and innate immune responses (phagocytic activity and lysozyme activity) in the juvenile sea cucumber *Apostichopus japonicas* [226].

6. Mode of Actions of Probiotic Fungi and Actinobacteria

Yeasts are an excellent source of β -glucan, which is well known for its role in immunostimulation in fish [227]. Yeasts are single-cell protein-rich organisms that can provide several essential vitamins (e.g., Vitamin B and folic acid), essential sulfur-containing amino acids (lysine) and diverse exo-enzymes for the degradation of complex food materials [228]. Along with bacteria and yeasts or other fungi, Actinomycetes are considered to be significant contributors to the breakdown and recycling of organic compounds [19]. Actinomycetes are known to produce many hydrolytic enzymes. Thus, the ecological role of actinobacteria as probiotics in aquaculture cannot be ignored. Like other probiotic microorganisms, actinobacteria were also reported with multiple functions, viz. improved water quality, immunity and growth in aquatic organisms [191]. Further, >50% of the microbial antibiotics are produced by Actinomycetes, of which *Streptomyces* and *Micromonospora* are by far the most common [229]. Although the specific modes of action of these microorganisms are inadequately described, like their limited applications in aquaculture, beneficial attributes documented for commonly used probiotics are expected to become applicable.

The modes of action of probiotics are well discussed in previous probiotic reviews, and several hypotheses have been suggested, which are summarized by Ringø et al. [1]. The recommended modes of action are as follows: (a) the competitive adhesion of probiotic microorganisms to epithelial receptors may prevent the attachment of pathogenic bacteria, (b) aggregation of probiotics and pathogenic bacteria preventing growth of the pathogenic organisms, (c) competition for nutrients between probiotic and undesired bacteria, (d) increased synthesis of lactic acid and the reduction in intestinal pH, (e) boost the production of specific antibacterial substances, (f) reduced production of toxic amines and decrease in the level of ammonia in the GI tract, (g) have beneficial effects on the intestinal immune system, (h) interference with quorum sensing, (i) act as a bioremediator, (j) enable improved defense against bacterial and viral infections, (k) alleviate adverse effects induced by crowding stress, and (l) improve antioxidant properties.

The suggested modes of action of the probiotic potential of fungi and actinobacteria likely to be effective in aquaculture are depicted in Figure 1.

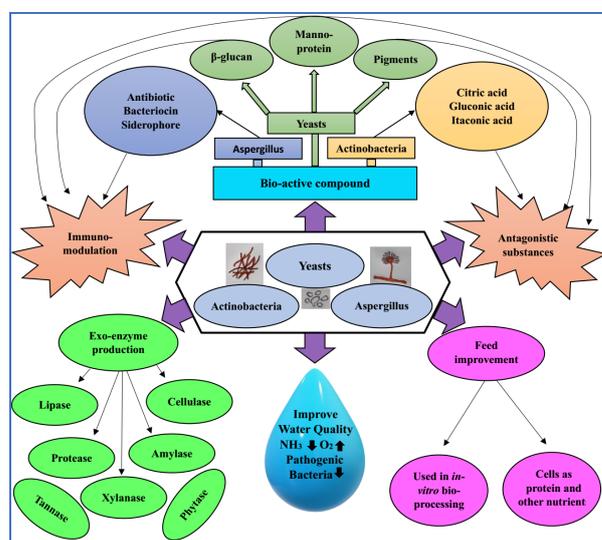


Figure 1. Probiotic potential of the fungi and actinobacteria studied.

7. Selection of Fungi and Actinobacteria as Probiotics

As proposed for bacterial probiotics [230], the selection criteria for the fungi or actinobacteria as putative probiotic organisms should consider functional and safety properties. Along with functionality, the colonization ability and viability of the primarily selected organisms should be considered. Indigenous or fish-gut-associated microorganisms have a better opportunity to colonize the host gut to exhibit probiotic effects. Thus, preference should be given to the autochthonous strains to search for probiotic fungi or actinobacteria, as the commensal organisms are believed to be well adapted to the anticipated ecological niche [231]. In addition, the habitat of the intended fish species can be considered a probable source of the beneficial microorganisms.

Yeast or other fungal strains can be isolated on YPD (1% yeast extract, 2% peptone, 2% dextrose) culture medium supplemented with antibiotics (chloramphenicol, 150 mg L⁻¹; tetracycline, 150 mg L⁻¹). As chloramphenicol and tetracycline typically inhibit the growth of Gram-positive and Gram-negative bacteria, the isolates that grew on the YPD media were likely fungi [111]. Fungal strains can be identified through 5.8S-ITS gene sequencing [232]. Alternatively, 18S rDNA gene sequence analysis may be followed [119]. The 'Internal Transcribed Spacer' (ITS) region in the 18S rDNA fragment can be amplified using ITS1 (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-30') as the forward and reverse primers.

To isolate actinobacteria, starch casein agar, Kuster's agar or actinomycete isolation agar medium may be used [233]. The supplementation of nalicidic acid (20 µg mL⁻¹) and nystatin/cycloheximide (100 µg mL⁻¹) will help to inhibit the growth of both Gram-negative bacteria and fungi [234]. Otherwise, the medium may be supplemented with streptomycin (25 µg mL⁻¹) to inhibit bacterial contamination. Actinobacteria may be identified through 16S rRNA gene sequence analyses. The gene encoding 16S rRNA may be amplified using 27f (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492r (5'-GGTACCTTGTTACGACTT-3') universal primers. The purified, amplified products may be sequenced, edited, aligned and analyzed to identify the closest homolog using the National Centre for Biotechnology Information (NCBI) GenBank database.

The assessment criteria for the selection of probiotic fungi [232] and actinobacteria [235] were demonstrated by considering the functional and safety properties, which are briefly presented in Figure 2. The following steps should be followed to select the probiotic strains:

- (a) Influence of temperature, pH and salt concentration (sodium chloride, NaCl) on growth;
- (b) Functional characterization, e.g., analyses of exo-enzyme production, antagonism against pathogenic bacteria, antioxidant activity, the production of short-chain fatty acids (SCFA) and vitamins, etc.;
- (c) Evaluation of growth and strain survivability against gut pH, pepsin, bile, and gut mucus;
- (d) Evaluation of colonization potential (co-cultivation with pathogens to test strain dominance and co-cultivation with other gut microorganisms to test strain compatibility, hydrophobicity, hydrophilicity and auto-aggregation assays);
- (e) Evaluation of safety assessment of strains through an antibiotic sensitivity test and hemolytic activity;
- (f) In vivo evaluation of the putative probiotic strains on the host via intra-peritoneal injection.

Further, it should be assured that the selected strains possess the following properties: (1) being non-pathogenic to the host; (2) being administrable through feed; (3) being effective in vivo; and (4) being non-virulent or possessing antibiotic resistance genes [230,236].

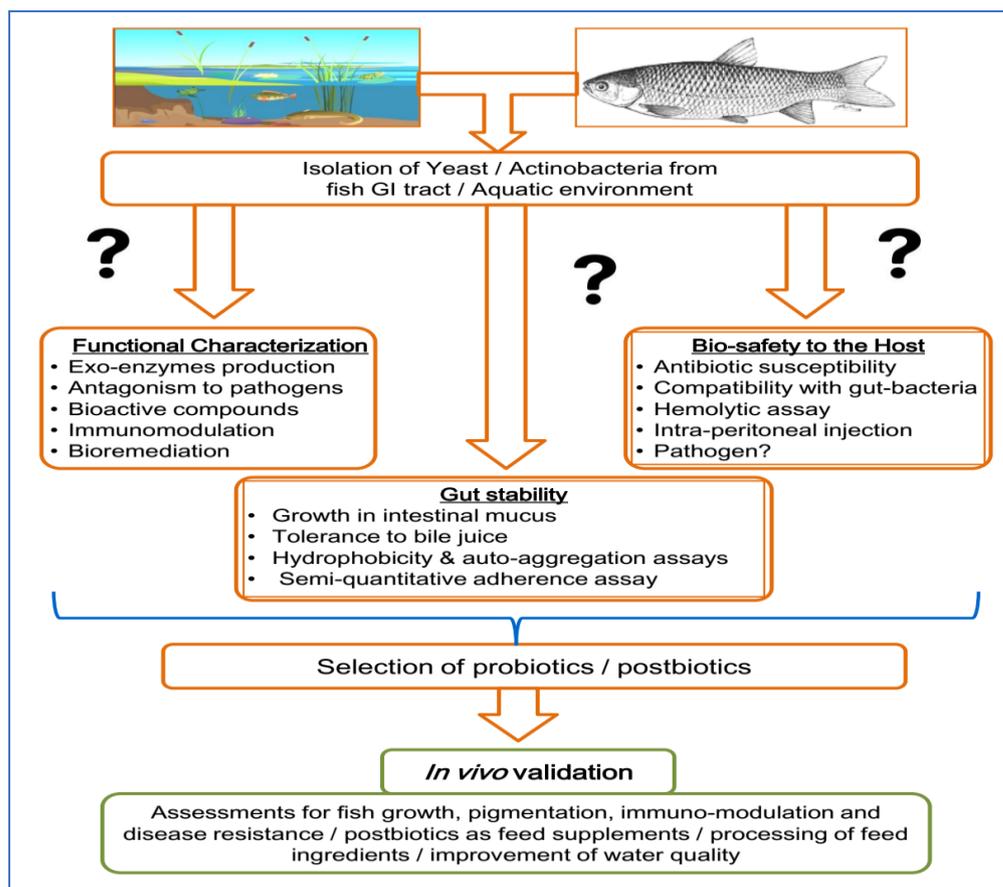


Figure 2. Proposed selection criteria of the probiotic fungi and actinobacteria.

8. Conclusions and Further Directions

Probiotic applications may be extended in aquaculture via the use of exo-enzyme-producing strains in the bioprocessing of the complex feed ingredients and diverse microbial bio-active compounds and/or metabolites (e.g., antimicrobial compounds, quorum quenching enzymes, SCFA) as functional feed additives. Further, apart from *S. cerevisiae*, gut-associated yeast strains of the genera *Candida*, *Pichia*, *Debaryomyces*, *Leucosporidium*, *Rhodotorula*, *Cryptococcus*, *Sporobolomyces* and *Trichosporon* have been described in several studies and need to be explored to determine their full potential. The vast diversity of marine actinobacteria and their novel metabolites were reported. Future research should be directed toward fish-gut-associated actinobacteria from freshwater and brackish water fish species to develop novel probiotics. Likely novel bioactive molecules from the diverse actinobacteria resources should also be considered. Apart from the antibacterial potential exhibited by the fungal and actinobacterial strains, their quorum quenching potential can be utilized to mitigate multidrug-resistant pathogens in aquaculture systems in an environmentally friendly way. Along with probiotic potential, studies should be directed to develop the probiotic products as synbiotics or postbiotics, and their efficacy in culture conditions must be evaluated. The development of paraprobiotics has not been widely considered with regard to fungi and actinobacteria, and this topic merits investigation, as paraprobiotics could represent safe and novel alternatives to the viable cells related to biofilm diseases. Studies addressing the impacts of putative probiotics on the gut microbiome and gut health are other developing areas that require appraisal of their efficacy. Moreover, efforts should be made to establish probiotic consortia comprising efficient and compatible bacteria–yeast–actinobacteria groups to address varied impediments in aquaculture systems. Available reports on probiotics' applications in diverse aquatic species suggest that the effects of probiotic candidates could be species specific in nature. Thus,

exploring the probiotic potential of the microbial candidates for the native commercial fish or other aquatic species in each region and deciphering this issue in feed and feeding technology are worth mentioning. Even though probiotics' inclusion in diet is the most frequently used administration method, studies need to be conducted to explore the potential of the water administration method. A simple question can be asked regarding fungi and other microorganisms in the fish GI tract: which species are present, and what do they do? Even though numerous probiotic studies of aquatic animals have been conducted, scientists must always ask this question.

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