frontiers | Frontiers in Marine Science

REVIEW
published: 02 June 2022
doi: 10.3389/fmars.2022.848037

Interesting Probiotic Bacteria Other Than the More Widely Used Lactic Acid Bacteria and Bacilli in Finfish

Einar Ringø[1]*, *Xuemei Li*[2], *Hien van Doan*[3] and *Koushik Ghosh*[4]

[1] Norwegian College of Fishery Science, Faculty of Bioscience, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway, [2] Key Laboratory of Freshwater Biodiversity Conservation, Ministry of Agriculture of China, Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Wuhan, China, [3] Department of Animal and Aquatic Sciences, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand, [4] Aquaculture Laboratory, Department of Zoology, The University of Burdwan, Burdwan, India

OPEN ACCESS

Edited by:
Benjamin Costas, University of Porto, Portugal

Reviewed by:
Ana Teresa Gonçalves, GreenCoLAB, Portugal
Francisco Vargas-Albores, Consejo Nacional de Ciencia y Tecnología (CONACYT), Mexico
Viswanath Kiron, Nord University, Norway

***Correspondence:**
Einar Ringø
Einar.Ringo@uit.no
orcid.org/0000-0002-4940-5688

Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *03 January 2022*
Accepted: *29 April 2022*
Published: *02 June 2022*

Citation:
Ringø E, Li X, Doan Hv and Ghosh K (2022) Interesting Probiotic Bacteria Other Than the More Widely Used Lactic Acid Bacteria and Bacilli in Finfish. Front. Mar. Sci. 9:848037. doi: 10.3389/fmars.2022.848037

Growing demands stimulate the intensification of production and create the need for practices that are both economically viable and environmentally sustainable. As European Union banned the use of antibiotics in production in 2003, several alternative treatments have been suggested, including probiotics. The first probiotic study in aquaculture was published in 1986, and since then probiotics have been considered as a beneficial tool in this industry. Today current evidence suggests that administration of certain probiotic strains might be able to enhance growth rate, improve the welfare of different fish species by modulating gut microbiota, improve physiological functions, such as metabolism, digestion, immunity, stress tolerance, intestinal histology, and disease resistance. Even though lactic acid bacteria and *Bacillus* spp. are the most frequently used probiotics in aquaculture, numerous studies have been published on other interesting probiotics. Therefore, the purpose of this paper is to summarize, comment, and discuss the current knowledge related to the effects of *Aeromonas*, *Aliivibrio*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Brochothrix*, *Clostridium*, *Enterovibrio*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodococcus*, *Rhodopseudomonas*, *Rhodosporidium*, *Roseobacter*, *Shewanella* and *Vibrio* as probiotics in finfish aquaculture, and present general information on their presence in the gastrointestinal tract of finfish. Moreover, some considerations for future studies are also indicated.

Keywords: probiotic bacteria, non-LAB, bacilli, finfish, aquaculture

INTRODUCTION

By 2025, aquaculture is expected to play a leading role in the global supply of fish. However, the growth of this industry could be considerably hampered by failures to predict, avoid, and contain infections. Unsurprisingly, the intensification of aquatic production has led to a significant increase in the frequency of disease and a growing inefficiency among the antibiotics used to treat these.

Antibiotics have been used in aquaculture for more than 50 years (Shamsuzzaman and Kumar, 2012), and previously the most common method for dealing with the occurrence of bacterial infections was the administration of antibiotics (Cabello, 2006; Cabello et al., 2020; Lulijwa et al., 2020), and the rapid growth of for example the Chilean salmon industry was accompanied by intensive use of antibiotics. However, as antibiotic administrations became the target of increasing public criticism and political controversy, Sweden was the first country in Europe, to ban the use of antimicrobial growth promoters as early as 1986. In 2003, European Union stated in Regulation (EC) No. 1831/2003; "*Antibiotics, other than coccidiostats or histomonostats, shall not be authorized as feed additives*". However, recent findings have revealed that mono- (e.g., Gudmundsdottir and Bjornsdottir, 2007) and polyvalent vaccines (e.g., Tobar et al., 2015) are effective for disease control in aquaculture, especially for salmonids. However, for many Chinese and Indian finfish-, shellfish- and cucumber species, vaccines are not available, and will hardly be available soon. However, there are several alternative treatment options available; phytobiotics, phage therapy, bacterial membrane vesicles (e.g., Jan, 2017; Tandberg et al., 2019; Mertes et al., 2021), quorum sensing interference, postbiotics (secreted by live bacteria, or released after bacterial lysis; Ang et al., 2020; Cuevas-González et al., 2020; Teame et al., 2020), postbiotics in combination with prebiotics, paraprobiotics (cell wall components; Taverniti and Guglielmetti, 2011; Choudhury and Kamilya, 2019; Nataraj et al., 2020), pro-, pre- and synbiotics. However, Cheng et al. (2014) argue that these "*so-called alternatives*" are not ideal antibiotics replacers.

According to Bermudez-Brito et al. (2012), "*Probiotics are live microorganisms that provide health benefits to the host when ingested in adequate amounts*". The probiotic concept is primarily based on the assumption that direct feeding of microbial cultures possesses beneficial effects on growth performance, digestive processes, the immune system and animal health. The use of probiotics gained attention within aquaculture in the mid 1980s (Kozasa, 1986), and since then numerous reviews papers have been published (e.g., Gatesoupe, 1999; Irianto and Austin, 2002a; Merrifield et al., 2010; Dimitroglou et al., 2011; Hoseinifar et al., 2018; Ringø et al., 2018; Wang et al., 2019a; Hoseinifar et al., 2020; Hu et al., 2020; Ringø et al., 2020a; Ringø et al., 2020b; Yao et al., 2020; Nayak, 2021; van Doan et al., 2021). In this context, it is also worth mention that administration of antibiotics lead to their accumulation in the tissues (Chen et al., 2020a), emergence of antimicrobial resistant bacteria in the environment (e.g., Marti et al., 2014; Chen et al., 2020a; Lulijwa et al., 2020), modulation of the gut microbiota (dysbiosis) (e.g., Ringø et al., 2016; Kim et al., 2019; Legrand et al., 2020), suppression of certain gut bacteria (Saettone et al., 2020), and increased abundance of intestinal bacteria that act as reservoirs for antibiotic resistance genes (Salyers et al., 2004; Saenz et al., 2019). In addition, modulation of the gut microbiota to an undesirable community can induce mucosal inflammation (Tamboli et al., 2004; Turroni et al., 2014). Furthermore, many antibiotics currently used in aquaculture are, or are closely related to agents used to treat bacterial diseases in humans, which makes their uncontrolled application in animal production an enormous risk to host health. It is thus clear that new methods to control aquatic infections is required.

Among the probiotic bacteria used in aquaculture are lactic acid bacteria (LAB) and *Bacillus* most frequently used (e.g., Ringø et al., 2018a; Kuebutornye et al., 2019; Soltani et al., 2019; Ringø et al., 2020a; Nayak, 2021; James et al., 2021; van Doan et al., 2021). However, in addition to LAB and bacilli are numerous probiotics such as *Aeromonas*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Brochothrix*, *Clostridium*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodococcus*, *Rhodopseudomonas*, *Rhodosporidium*, *Roseobacter*, *Shewanella* and *Vibrio* used.

The use of probiotics is an alternative approach to reduce pathogen adherence and colonization in larval-, fry- and juvenile intestines by modulating the intestinal microbiota with beneficial bacteria. They can be added to the diet or water in order to enhance the proportion of health-promoting bacteria in the gut. An advantage of this method is that it can be implemented during the early stages of development when vaccination by injection is impractical.

The review of Irianto and Austin (2002a); Tapia-Paniagua et al. (2012); De et al. (2014); Newaj-Fyzul et al. (2014), Tan et al. 2020), Cámara-Ruiz et al. (2020); Hayatgheib et al. (2020), and van Doan et al. (2021) presented some information on administrations of the probiotic bacteria discussed in the present study, and to avoid duplication with that presented in the above mention reviews, these studies are only briefly presented in Tables.

The present review address to present an overview of interesting probiotic bacteria, not LAB and bacilli, with focus on growth performance, modulation of the gut microbiota, gut histology, effect on immunesystem, and disease resistance in finfish. Furthermore, some general information is presented on the probiotics discussed, and their presence in the GI tract of finfish.

ADMINISTRATION AND MODE OF ACTIONS

Probiotic administration has been described in several reviews (e.g., Verschuere et al., 2000; Irianto and Austin, 2002a; Villamil et al., 2010; Dawood and Koshio, 2016; Kumar et al., 2016; Hoseinifar et al., 2018; Jahangiri and Esteban, 2018; Ringø et al., 2020a; Vargas-Albores et al., 2021), and in order to avoid overlaps, the administration methods are only briefly presented.

i) Oral administration *via* diet or water/bath, *ii*) Administration of several probiotics in combination (Fuller, 1989; Kesarcodi-Watson et al., 2012; Melo-Bolivar et al., 2021), *iii)* Inactivated bacteria, *iv*) Spores, *v*) Culturing, and added to feed as freeze-dried cultures, which sometimes are coated with lipids, *vi*) Encapsulation e.g., by calcium alginate beads (e.g.,

Rosas-Ledesma et al., 2012; Cordero et al., 2015; Prado et al., 2020), *vii)* Lyophilization, *viii*) Administration – continuously or regular intervals, but are the probiotics permanently colonisers in the GI tract, *ix*) Co-administration of probiotics with prebiotics or plant products, and x) Host specificity, or strains from other species or commercial probiotics (Lazado et al., 2015; van Doan et al., 2020).

The modes of action of probiotics are well discussed, and several hypotheses have been suggested (e.g., Irianto and Austin, 2002a; Prado et al., 2010; Kumar et al., 2016; Zorriehzahra et al., 2016; Wang et al., 2017; de Melo Pereira et al., 2018; Hoseinifar et al., 2018; Chauhan and Singh, 2019; Ran et al., 2021), and according to these reviews the modes of action are: a) competitive adhesion of probiotic microorganisms to epithelial receptors may prevent the attachment of pathogenic bacteria (rational behind "*competitive exclusion*"), b) aggregation of probiotics and pathogenic bacteria, c) competition for nutrients between probiotic and undesired bacteria, d) increased synthesis of lactic acid and reduction of intestinal pH, e) production of specific antibacterial substances, f) reduced production of toxic amines and decrease of ammonia level in the GI tract, g) beneficial effects on the intestinal immune system, h) interference with quorum sensing, i) bioremediator, j) improved defense against bacterial and viral infections, k) alleviate negative effects induced by crowding stress, and l) antioxidant properties.

GRAM-NEGATIVES

In **Table 1** are the beneficial effects of Gram-negative probiotic bacteria used in finfish aquaculture revealed. In addition, some vital information is presented from *in vitro* studies.

Acinetobacter

Acinetobacter belong to Gammaproteobacteria, is oxidase-negative, aerobic coccobacilli with twitching motility. They are isolated from the GI tract of finfish (e.g., Ringø et al., 2006a; Navarrete et al., 2013; Liu et al., 2019; Wang et al., 2020a), but their use as probiotics in finfish are less investigated (Bunnoy et al., 2019a), and as a part in multi-strain probiotic supplementation (Li et al., 2019a).

In a study with bighead catfish (*Clarias macrocephalus*; 150g), Bunnoy et al. (2019a) used an *Acinetobacter* originally isolated from skin mucus of bighead catfish revealing strong antibacterial activity against several freshwater pathogens *in vitro* (Bunnoy et al., 2019b). After 15- and 30-days administration, phagocytic index, phagocytic-, lysozyme-, and respiratory burst activity, and alternative complement pathway significantly enhanced, and upregulation of immune-related genes was observed. After 30 days administration, increased resistance was observed following intraperitoneal injection with *Aeromonas hydrophila.* The main reason why *Acinetobacter* species have little been used as probiotics in finfish, may be due to reports on opportunistic fish pathogenic agents within the genus.

Aeromonas

Aeromonas is facultative anaerobic, rod-shaped bacteria. Even though *Aeromonas* are mainly associated with diseases (Feckaninova et al., 2017), there are present in the GI tract of healthy finfish (e.g., Ringø et al., 1997; Navarrete et al., 2013; Chen et al., 2014; Abdelhamed et al., 2019). In finfish, information is available on the use of *Aeromonas* as probiotics (Irianto and Austin, 2002b; Lategan et al., 2004; Brunt and Austin, 2005; Makridis et al., 2005; Brunt et al., 2007; Brunt et al., 2008; Makridis et al., 2008; Pieters et al., 2008; Abbass et al., 2010; Wu et al., 2015; Hao et al., 2017), as well as a part of multi strains probiotics supplementation; *Aeromonas veronii* in combination with *Flavobacterium sasangense* (Chi et al., 2014).

Irianto and Austin (2002b) indicated that feed supplemented with *A. hydrophila* for 7 and 14 days led to better survival rate of rainbow trout (*Oncorhynchus mykiss*) following challenge with *Aeromonas salmonicida*. In contrast, Makridis et al. (2005) revealed no clear effect on survival of gilthead sea bream (*Sparus aurata*) larvae exposed to 6 x 10^5 *Aeromonas* mL^{-1}.

Saprolegina paracitica (saprolegniosis; caused by fungal infections) is reported in silver perch (*Bidyanus bidyanus*), and Lategan et al. (2004) revealed that administration of *Aeromonas media* strain A199 to the tank water of silver perch halted the outbreak. In three later studies using *Aeromonas sobria* GC2 as probiont to rainbow trout, Brunt and Austin (2005) and (2008); Brunt et al. (2007) revealed enhanced survival after challenge with a range of pathogens. Similarly, Pieters et al. (2008) displayed that dietary inclusion of *A. sobria* protected rainbow trout against surface infections and against a eukaryotic pathogen, *Ichthyophthirius multifiliis*. Abbass et al. (2010) evaluated intraperitoneal and intramuscular injections of subcellular component of *A. sobria* GC2 to rainbow trout and revealed protection against *Yersinia ruckeri*.

Even though, diseases caused by *A. veronii* in freshwater fish are reported (e.g., Liu et al., 2018), the bacterium has been used as probiotic supplement. A dietary supplementation of *A. veronii* isolated from grass carp (*Ctenopharyngodon idella*) was administrated to grass carp, 10^8 CFU g^{-1}, for 28 days and challenged with *A. hydrophila* (Wu et al., 2015). A significant increase of respiratory burst, phagocytic and lysozyme activities, and upregulation of immune related genes (*IL-8*, *IL-1β*, *lysozyme-C* and *TNF-α*), and resistance against *A. hydrophila* were observed. Modulation of the gut microbiota of grass carp by *A. veronii* administration was revealed by Hao et al. (2017), as *Brevundimonas* was the abundant genus in the GI tract, while *Lactococcus*, *Pseudomonas* and *Vibrio* decreased, and *Flavobacterium* and *Lactococcus* was not detected in probiotic administrated fish compared to control fed fish.

Alcaligenes

A genus of rod-shaped, motile, aerobic bacteria, and some strains of *Alcaligenes* are capable of anaerobic respiration in the presence of nitrate or nitrite. The genus does not use carbohydrates. Strains of *Alcaligene*s are reported in the intestinal tracts of vertebrates as well as finfish (e.g., Ringø, 1993; Navarrete et al., 2013; Sedlacek et al., 2016; Karlsen et al., 2017).

A decapeptide (cyclo-(l-Pro-Gly)5) from *Alcaligenes faecalis* revealed immunostimulatory activities in a study with crucian carp (*Carassius carassius*) (Wang et al., 2011), and a challenge experiment displayed that fish injected with the decapeptide

TABLE 1 | Effect of Gram-negative bacteria on growth performance, gut health, immune system and disease resistance in finfish, and some *in vitro* studies.

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
Acinetobacter KU011TH	Skin mucus of bighead catfish	10^5, 10^7, 10^9 CFU g^{-1}, 30 days	Bighead catfish ~ 150 g	↑ growth performance, upregulated expression of several immune-related gens and resistance against *Aeromonas hydrophila* → histopathological changes in gills, skin, intestine or liver	Bunnoy et al. (2019a)
Acinetobacter sp. P27 and P33	Yellowtail amberjack	*In vitro* test	*In vitro* test	↑ antimicrobial activity against *Vibrio* 25LT1	
Aeromonas sp.	Isolated from live feed	6 x 10^5 CFU mL^{-1}, 10 days	Gilthead sea bream larvae	Survival was similar to those larvae held in sterilized seawater	Makridis et al. (2005; 2008)
Aeromonas hydrophila A3-51	Fish intestine, no specification	Deal cells, 10^7 cells g^{-1}, 21 days	Rainbow trout ~ 1 g	↑ survival against *Aeromonas salmonicida* and larger number of erythrocytes vs. control → numbers of leucocytes and lysozyme activity	Irianto and Austin (2003a)
A. hydrophila A3-51	Fish intestine, no specification	Inactivated A3-51, 2 x 10^7 cells g^{-1}, 84 days	Goldfish, 40 – 50 mm in length	↑ survival against *A. salmonicida* and larger number of erythrocytes and leucocytes vs. control	Irianto and Austin (2003b)
Aeromonas media A199	Cultured collection	Administration to water, 10^4 -10^5 cells mL^{-1}, 3 weeks	Silver perch, 200 – 300 g	Administration halted outbreak of saprolegniosis	Lategan et al. (2004)
Aeromonas sobria GC2	Ghost carp	10^3, 10^6, 10^7 and 10^{10} CFU g^{-1}, 14 days	Rainbow trout ~ 20 g	↑ resistance against *Lactococcus garvieae* and *Streptococcus iniae*	Brunt and Austin (2005)[1]
A. sobria GC2	Ghost carp	2 x 10^8 CFU g^{-1}, 14 days	Rainbow trout ~ 12 g	↑ lysozyme, phagocytic and respiratory activity, and resistance against *Aeromonas salmonicida*, *Lac. garvieae*, *S. iniae*, *V. anguillarum*, *Vibrio ordalli* and *Yersinia ruckeri*	Brunt et al. (2007)
A. sobria GC2	Ghost carp	10^3, 10^6, 10^7 and 10^{10} CFU g^{-1}, 14 days	Rainbow trout ~ 25 g	↑ NADH dehydrogenase, dystrophin, mKIAA0350	Brunt et al. (2008)
A. sobria GC2	Ghost carp	10^8 CFU g^{-1}, 14 days	Rainbow trout ~ 25 g	↑ phagocytic activity and resistance against *Aeromonas bestiarum*, bacterium cause skin infection	Pieters et al. (2008)[1,2]
Subcellular component of *Aeromonas sobria* GC2	Unknown, laboratory strain, parabiotics of GC2	Intraperitoneal- or intramuscular injection	Rainbow trout ~ 12 g	↑ resistance against *Y. ruckeri*	Abbass et al. (2010)
Aeromonas veronii A-7	Grass carp	10^8 CFU g^{-1}, 28 days	Grass carp 35 ± 5 g	↑ non-specific immune parameters, immune-related genes, and resistance against *A. hydrophila*	Wu et al. (2015)
Aeromonas veronii A-7	Grass carp	10^8 CFU g^{-1}, 28 days	Grass carp 40 ± 0.5 g	Modulated the gut microbiota	Hao et al. (2017)
Alcaligenes sp.	Malaysian Mahseer	10^8CFU g^{-1}, 90 days	Malaysian Mahseer ~ 1.4 g	↑ weight gain, gut histology, and short chain fatty acids in the gut Modulated the gut microbiota	Asaduzzaman et al. (2018)
Alcaligenes faecalis Y311	Sediment of tilapia tank	10^8 CFU mL^{-1}, every 7 days over 3 months	Nile tilapia ~ 5.2 g	↑ alkaline phosphatase activities in gill and intestine → on the dominant bacteria, but some low-abundance bacteria in skin, gill and intestine was affected ↓ relative abundance of *Acinetobacter* in the gut	Wang et al. (2020a)
Alteromonas sp.	European sea bass	10^5 and 10^8 CFU mL^{-1}, inoculated intraperitoneally	European sea bass, 354 ± 83 g	↑ immunostimulative properties	Mladineo et al. (2016)
Chromobacterium aquaticum	Lake water	10^6, 10^7 CFU g^{-1}, 8 weeks	Zebrafish ~ 4.7 g	↑ hepatic mRNA expression of carbohydrate metabolism-related genes, growth related genes, resistance against *A. hydrophila* and *Streptococcus iniae* Induced innate immune-related genes	Yi et al. (2019)
Enterobacter strain PIC15 and *Enterobacter amnigenus*	Rainbow trout	10^6 – 10^8 CFU g^{-1}, 7 days	Rainbow trout ~ 5 g	↑ resistance against *Flavobacterium psychrophilum*	Burbank et al. (2011)
Enterobacter sp. JC10	No information given	5 x 10^4 CFU g^{-1}, 30 days	Red tilapia, 35-40g	→ growth, survival and feed convention rate Adhesion experiment showed adherence abilities	Suryaningsih et al. (2021)
Enterobacter cloacae	Curd (coagulating milk)	10^7 CFU g^{-1}, 60 days	Kenyi cichlid ~ 1.5 g	↑ growth, respiratory burst activity Modulated the gut microbiota	Girijakumari et al. (2018)
Phaeobacter sp.	Turbot hatchery	10^7 CFU mL^{-1} added to well dishes	Atlantic cod larvae	↑ resistance against *Vibrio anguillarum* 02α	D´Alvise et al. (2013)

(Continued)

TABLE 1 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
Phaeobacter sp.	Turbot hatchery	Grown on ceramic biofilter (probiofilter)	Turbot* larvae	↑ resistance against *V. anguillarum*, and seawater quality → gut microbiota	Prol-García and Pintado (2013)
Phaeobacter gallaeciensis	Seawater in scallop cultures	10^7 CFU mL^{-1}	Atlantic cod larvae	↑ resistance against *V. anguillarum* serotype 01	D´Alvise et al. (2012)
Phaeobacter inhibens DSM 17395	Mariculture environment	4.05 x 10^6 ± 1.05 10^6 CFU per cell	Turbot larvae	→ gut community structure ↓ relative abundance of Rhodobacterales in the gut	Dittmann et al. (2020)
Pseudoalteromonas AP5	Clownfish	10^5 mL^{-1}	Clownfish larvae	↑ survival Partially out compete *V. alginolyticus* in the gut	Vine (2004)
Pseudoalteromonas sp.	European sea bass	10^5 and 10^8 CFU mL^{-1}, inoculated intraperitoneally	European sea bass, 354 ± 83 g	↑ immunostimulative properties	Mladineo et al. (2016)
Pseudomonas sp.	NI	10^7 CFU g^{-1}, 90 days	Nile tilapia ~ 21 g	→ growth performance, and hematological and biochemical parameters ↓ resistance against *A. hydrophila*	Abd El-Rhman (2009)[3]
Pseudomonas M174	Rainbow trout egg	Bathing	Rainbow trout ~ 15 g	Potential as probiotic against *Flavobacterium psychrophilum*	Korkea-aho et al. (2012)[3]
Pseudomonas MSB1	Rainbow trout	*In vitro* test	*In vitro* test	Produced siderophores	Strom-Bestor and Wiklund (2011)[3]
Pseudomonas sp. P18	Yellowtail amberjack	*In vitro* test	*In vitro* test	↑ antimicrobial activity against *Vibrio* 25LT1, *Vibrio* 25LH1, and *Vibrio* 25LS1	
Pseudomonas aeruginosa VSG2	Rohu gut content	10^5, 10^7, 10^9 CFU g^{-1}, 60 days	Rohu ~ 60 g	↑ serum lysozyme↑- and alternative complement pathway activities, phagocytosis, respiratory burst activity in head kidney macrophages, and superoxide dismutase and resistance against *A. hydrophila* at $10^7$and 10^9 inclusions	Giri et al. (2012)[2]
P. aeruginosa VSG2	Rohu gut content	Cellular component of *P. aeruginosa*, intraperitoneal	Rohu ~ 43.5 g	↑ respiratory burst-, phagocytic- activities, expression of immune-related genes, and survival against *A. hydrophila*	Giri et al. (2015)
P. aeruginosa VSG2	Rohu gut content	Heat-killed *P. aeruginosa* VSG2	*In vitro*, head kidney macrophages were isolated from rohu ~ 190 g	↑ cytokine expression	Giri et al. (2016)
P. aeruginosa	Skin mucus of catfish	10^7 CFU mL^{-1}, challenge in a biocontrol study, with or without co-habitation of *A. hydrophila*-15 min	Rohu, fingerlings	*In vitro* immunomodulation ↑ survival against *A. hydrophila*	Hoque et al. (2019)[2]
P. aeruginosa VSG2	Indian major carp	Heat-killed VSG2, 20 and 40 mg kg^{-1}, 8 weeks	Common carp ~ 6.5 g	↑ immune system, antioxidant efficacy, and resistance against *A. hydrophila*	Giri et al. (2020)
Fluorescent pseudomonad F19/3 (*Pseudomonas fluorescens*)	Atlantic salmon	Bathing in bacterial suspension	Brown trout	↑ resistance against *A. salmonicida*	Smith and Davey (1993)
P. fluorescens AH2	Iced freshwater fish	Addition to rearing water, 10^7 CFU mL^{-1}, 5 days	Rainbow trout ~ 40 g	↑ growth rate and survival following challenge with *V. anguillarum*	Gram et al. (1999)[3,4]
P. fluorescens AH2	Iced freshwater fish	10^3–10^5 CFU mL^{-1} rearing water, 5 days	Atlantic salmon 20 – 25 g	→ effects against infection with *Aeromonas salmonicida*	Gram et al. (2001)
P. fluorescens LE89 and LE141	Skin of brown trout, LE89, and LE141 from rainbow trout skin	Adding the strains to water, final concentration of 10^6 CFU mL^{-1}	Rainbow trout ~ 16 g	Reduced saprolegniosis-a disease caused by pseudo-fungus	González-Palacios et al. (2019)
P. fluorescens LE89 and LE141	Skin of brown trout, LE89, and LE141 from	Adding the strains to water, final concentration of 10^6 CFU mL^{-1}	Rainbow trout, 72 ± 10 g	↑ innate immune response and reduced saprolegniosis	González-Palacios et al. (2020)

(Continued)

TABLE 1 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
	rainbow trout skin				
Pseudomonas monteilii JK-1	Grass carp gut	Dietary administration, 7 days	Grass carp ~ 20 g	Not toxic to grass carp → effects against infection with *A. hydrophila*	Qi et al. (2020)
Pseudomonas stutzeri F11	Grass carp pond	10^5 CFU mL^{-1}, 3 day intervals	Grass carp ~ 16 g	Reduced levels of ammonia-N, nitrite-N and total N in water, and modulated the water microbiota	Fu et al. (2017)
Psychrobacter sp.	Grouper intestine	10^8 CFU mL^{-1}, 60 days	Grouper ~ 45 g	↑ feed conversion ratio and serum component 4 → weight gain, specific growth rate, hepatopancreatic protease and lipase activity, intestinal amylase activity, and immune parameters	Sun et al. (2011)
Psychrobacter namhaensis	Marine environment	2.8 x 10^7, 5.6 x 10^7 CFU mL^{-1}, 50 days	Nile tilapia ~ 4.6 g	↑ growth, hematocrit-, hemoglobin-, erythrocytes-, total leucocyte values ↑ immunoglobulin, alternative hemolysis, phagocytic and lysozyme activities by the 2.8 x 10^7 CFU mL^{-1} feeding	Makled et al. (2017)
Psychrobacter maritimus S	Sediment	3.3 x 10^8, 6.6 x 10^8 CFU mL^{-1}, 50 days	Nile tilapia ~ 5.4 g	↑ growth, digestive enzymes, phagocytic- and lysozyme activity, alternative complement hemolysis, hematological parameters, and expression of interleukin-4 and 12 was upregulated by 3.3 x 10^8 CFU mL^{-1} feeding	Makled et al. (2020)
Rhodopseudomonas palustris (photosynthetic bacteria)	Common carp	10^7 CFU mL^{-1}, was added to the rearing water every 2 day, 40 days	Nile tilapia ~ 7 g	↑ growth performance, respiratory burst-, superoxide dismutase,- catalase- and myeloperoxidase activities → total serum protein, albumin, globulin, serum lysozyme content	Zhou et al. (2010)
R. palustris	Common carp pond	10^6 CFU g^{-1}, 60 days	Grass carp ~ 2.1 g	↑ growth performance, and amylase activity in proximal- and distal intestine → protease- and cellulase activity in proximal- and distal intestine	Wang (2011)
R. palustris	Grass carp pond	10^{11} CFU/m^3 per week, 15 days	Grass carp ~ 15 g	↓ ammonia-N, total inorganic-N and total-N Modulated the water microbiota	Zhang et al. (2014)
R. palustris	NI	Six days wastewater treatment	Yellow catfish, 30 ± 5 g	↑ digestive enzyme activities, and immune enzyme-related gene, antioxidant enzyme-related gene expression, and resistance against *A. hydrophila* Modulated the gut microbiota	Liu et al. (2020)
Roseobacter sp. 27-4**	Tank wall of turbot hatchery	Addition to rearing water	Turbot larvae	↓ mortality	Hjelm et al. (2004)[3]
Roseobacter sp. 27-4**	Tank wall of turbot hatchery	Enriched rotifers with 27-4, 10 days	Turbot larvae	↑ survival against *V. anguillarum* and 27-4 was detected in gastrointestinal lumen	Planas et al. (2004)
Roseobacter sp.	Isolated from live feed	6 x 10^5 CFU mL^{-1}, 10 days	Gilthead sea bream larvae	Survival was similar to those larvae held in sterilized seawater	Makridis et al. (2005; 2008)
Shewanella sp.	Isolated from live feed	6 x 10^5 CFU mL^{-1}, 10 days	Gilthead sea bream larvae	Survival was similar to those larvae held in sterilized seawater	Makridis et al. (2005; 2008)[5]
Shewanella sp. MR-7	Intestinal mucus of turbot	Soybean meal fermented by MR-7, 79 days	Turbot ~ 7.6 g	→ effects on digestive enzymes activities Suppressing inflammatory responses, and modulated the intestinal microbiota	Li et al. (2019b)
Shewanella sp. MR-7	Intestinal mucus of turbot	~ 10^8 CFU g^{-1}, 7 days	Turbot ~ 71 g	↑ intestinal villus and microvilli height, inflammatory response Modulated the gut microbiota	Zhang et al. (2020)
Shewanella sp.	Malaysian Mahseer	10^8CFU g^{-1}, 90 days	Malaysian Mahseer ~ 1.4 g	↑ gut histology, short chain fatty acids in the gut, and modulated the gut microbiota	Asaduzzaman et al. (2018)
Shewanella baltica Pdp13	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 60 days	Senegalese sole 10-17 g	↑ growth and resistance against *Photobacterium damselae* sub. *piscicida* → kidney leucocytes respiratory burst activity	Díaz-Rosales et al. (2009)[4]
S. baltica	Yellowtail amberjack	*In vitro* test	*In vitro* test	↑ antimicrobial activity against *Vibrio* 25LT1, *Vibrio* 25LH1	
Shewanella putrefaciens Pdp11	Skin mucus of gilthead seabream	Heat-inactivated Pdp11, 60 days	Gilthead seabream ~ 65 g	↑ phagocytic ability of head kidney leucocytes	Díaz-Rosales et al. (2006)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Heat-inactivated Pdp11	Gilthead seabream ~ 65 g	↑ cellular innate immune responses	Salinas et al. (2006)[5,6]

(Continued)

TABLE 1 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 60 days	Senegalese sole 10-17 g	↑ growth, kidney leucocytes respiratory burst activity and resistance against *Photobacterium damselae* sub. *piscicida*	Díaz-Rosales et al. (2009)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 60 days	Senegalese sole 10-15 g	↑ growth performance, the length of microvilli → proximal composition ↓ lipid droplets inside the enterocytes	Sáenz de Rodrigáñez et al. (2009)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 60 days	Senegalese sole 26.7± 4.6 g	↑ kidney leucocytes respiratory burst activity and resistance against *Photobacterium damselae* sub. *piscicida* ↓ lipid droplets inside the enterocytes	Garcia de la Banda et al. (2010)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Live (10^9 calls g^{-1}) or lyophilized cells of Pdp11, 60 days	Senegalese sole ~ 30 g	Modulated the intestinal microbiota	Tapia-Paniagua et al. (2010)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 116 days	Gilthead seabream ~ 38.5 g	↑ stress tolerance	Varela et al. (2010)[5,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Live (10^9 calls g^{-1}) or lyophilized cells of Pdp11, 2 months	Senegalese sole ~ 23.5 g	↑ growth (live bacteria), and resistance against *Photobacterium damselae* sub. *piscicida* (both treatments) → growth (lyophilized)	García de la Banda et al. (2012)[3,6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Enrichment of *Artemia* (2.5 x 10^7 CFU mL^{-1}), 90 days post hatching	Senegalese sole larvae	↑ growth Modulated the gut microbiota	Lobo et al. (2014a)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Enrichment of *Artemia* (2.5 x 10^7 CFU mL^{-1}), 119 days after hatching	Senegalese sole larvae	↑ growth performance, proteolytic activity, and modulation of the gut microbiota	Lobo et al. (2014b)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Enrichment of *Artemia* metanauplii, 10-30 days post hatching	Senegalese sole larvae	Modulated the gut microbiota	Tapia-Paniagua et al. (2014a)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 30 days	Senegalese sole ~ 15 g	Modulated the gut microbiota under stress	Tapia-Paniagua et al. (2014b)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 4 weeks	Gilthead seabream ~ 14.5 g	↑ some immune responses and gene expression → growth performance	Guzmán-Villanueva et al. (2014)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 4 weeks	Gilthead seabream ~ 8 g	↑ carbohydrate composition and up-regulated different immune-related gene expression in skin	Cerezuela et al. (2016)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Encapsulated in calcium alginate beads (10^8 CFU g^{-1}), 4 weeks	Gilthead seabream ~ 44 g	↑ humoral parameters Modulated gut microbiota	Cordero et al. (2015)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^8 CFU g^{-1}, 4 weeks	Gilthead seabream, no information given about fish weight	↑ cellular, humoral immunity and gene expression profile of pro-inflammatory cytokines	Cordero et al. (2016a)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Skin samples were incubated by 10^3 mL^{-1}, of Pdp11 and *P. damselae* in 12 well plates for 2 hours	Gilthead seabream ~ 97 g	Different patterns of cytokine profile in dorsal and ventral skin	Cordero et al. (2016b)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^8 CFU g^{-1}, 30 days	Gilthead seabream ~ 108 g	↑ skin mucosal immunity.	Cordero et al. (2016c)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	*Artemia* metanauplii as vector (2.5 x 10^7 CFU mL^{-1}), 119 days after hatching	Senegalese sole larvae	↑ growth until day 87 post hatching Sole lipid profile was affected	Lobo et al. (2016)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 15 days thereafter control diet for 6 days	Senegalese sole, 26.7 ± 4.6 g	↑ protective effect against oxidative stress Modulation of the gut microbiota	Vidal et al. (2016)[6]

(Continued)

TABLE 1 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	Mixed diets of commercial formulated feed and live prey (rotifers and *Artemia*), 73 days post hatching	Senegalese sole larvae	↑ total protein concentration, alkaline phosphatase activity, non-specific immune response Effects larval development and gene expression	Jurado et al. (2018)[6]
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 30 days	Gilthead seabream ~ 22 g	Administration facilitated wound closure ↑ albumin/globulin ratio, protease and peroxidase activities in skin mucus, and anti-inflammatory cytokines (*il-10* and *tgf- β*), 7 days after post-wounding ↓ serum aspartate aminotransferase and pro-inflammatory cytokines (*il-1 β, il-6, il-8* and *tnf-α*).	Chen et al. (2020b)
S. putrefaciens Pdp11	Skin mucus of gilthead seabream	10^9 CFU g^{-1}, 30 days	Gilthead seabream ~ 22 g	Up-regulation of pro-inflammatory cytokines, while the tight junction protein *occluding* was down-regulated → number of goblet cells	Chen et al. (2020c)[6]
Shewanella xiamenensis A-1 and A-2	Grass carp	10^8 CFU g^{-1}, 28 days	Grass carp 35 ± 5 g	↑ non-specific immune parameters, immune-related genes, and resistance against *A. hydrophila*	Wu et al. (2015)
S. xiamenensis A-1	Grass carp	10^8 CFU g^{-1}, 28 days	Grass carp 40 ± 0.5 g	Modulated the gut microbiota	Hao et al. (2017)
Allivibrio	Atlantic salmon	Different concentrations of the probiotics were added to the tanks, 4-6 months	Atlantic salmon, 55, 88 and 110 g in the various trials	↑ growth performance and ulcer prevalence	Klakegg et al. (2020a)
Enterovibrio coralii	European sea bass	10^5 and 10^8 CFU mL^{-1}, inoculated intraperitoneally	European sea bass, 354 ± 83 g	→ immunostimulative properties	Mladineo et al. (2016)
	Atlantic salmon	Bathing in bacterial suspension, varied from 7.5 x 10^5 to 5 x 10^7 for 10-30 min	Lumpfish, 0.025 to 16.3 g in the various trials	Fewer ulcer outbreak caused by *Moritella viscosa*	Klakegg et al. (2020b)
Strain E (*Vibrio alginolyticus* – like)	Turbot larvae	Enrichment of rotifer	Turbot larvae	↑ resistance against *Vibrio* strain P	Gatesoupe (1997)[3]
Vibrio strain PB 1-11 and PB 6-1	Atlantic halibut juveniles	Enrichment of rotifer	Atlantic halibut larvae	↑ total CFU in water → larval gut microbiota	Makridis et al. (2001)
Vibrio alginolyticus	Commercial shrimp hatchery	Bathing in bacterial suspension ~ 10^8 CFU mL^{-1}	Atlantic salmon ~ 21 g	↑ survival when challenge *with A. salmonicida*, but to a lesser extent after exposure to *V. anguillarum* and *Vibrio ordalli* The probiont was revealed in the intestine up to 21 days after initial application	Austin et al. (1995)[3]
Vibrio fluvialis A3-47S	Fish intestine, no specification	Deal cells, 10^7 cells g^{-1}, 21 days	Rainbow trout ~ 1 g	↑ survival against *A. salmonicida* → numbers of erythrocytes and leucocytes and lysozyme activity	Irianto and Austin (2003a)[2]
Vibrio lentus	Sea bass larvae	10^6 CFU mL^{-1} well water, 8 days post hatching	Gnotobiotic sea bass larvae	↑ resistance against *V. harveyi*	Schaeck et al. (2016)
Vibrio lentus	Sea bass larvae	10^6 CFU mL^{-1} well water, 8 days post hatching	Gnotobiotic sea bass larvae	↑ gene expression → apoptotic and cell proliferative indexes	Schaeck et al. (2017)
V. lentus	Sea bass larvae	10^6 CFU mL^{-1} well water, 8 days post hatching	Gnotobiotic sea bass larvae	Lower glucocorticoid levels in larvae	Aerts et al. (2018)
Vibrio pelagius	Copepod fed turbot larvae	Addition to rearing water, 4x10^5 CFU mL^{-1}, 14 days	Turbot larvae	Modulated gut microbiota	Ringø et al. (1996)
V. pelagius	Copepod fed turbot larvae	Addition to rearing water, 10^5 CFU mL^{-1}, 16 days	Turbot larvae	↓ mortality when challenge with *Aeromonas caviae*	Ringø and Vadstein (1998)[3]
V. pelagius	Copepod fed turbot larvae	Addition to rearing water, 10^5 CFU mL^{-1}, 16 days	Turbot larvae	*V. pelagius* colonize the intestine → survival	Ringø (1999)
Vibrio proteolyticus	No information given	Oral intubation 10^{10} CFU mL^{-1}, diet-water mixture, 3weeks	Turbot 25-30 g	↑ protein digestion	DeSchrijver and Ollevier (2000)
V. proteolyticus	Sea bass larvae	10^8 CFU mL^{-1} well water, 8 days post hatching	Gnotobiotic sea bass larvae	→ against *V. harveyi* infection	Schaeck et al. (2016)

(Continued)

TABLE 1 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
Vibrio iliopiscarius	No information given	10^5 CFU mL^{-1}	Atlantic halibut larvae	↓ larval survival, 32 days post hatched	Ottesen and Olafsen (2000)
Apathogenic *Vibrio salmonicida*	No information given	10^5 CFU mL^{-1}	Atlantic halibut larvae	↑ larval survival, 32 days post hatched	Ottesen and Olafsen (2000)

↑ - increased; → no effect; ↓ - decrease.
IP, intraperitoneal injection; IM, intramuscular injection.
** reclassified as Phaeobacter strain 27-4 by Prol et al. (2009).
Bighead catfish (Clarias macrocephalus); Yellowtail amberjack (Seriola lalandi); Gilthead sea bream (Sparus aurata); Rainbow trout (Oncorhynchus mykiss); Goldfish (Carassius auratus); Silver perch (Bidyanus bidyanus); Ghost carp (Cyprinus carpio albino); Grass carp (Ctenopharyngodon idella); Malaysian Mahseer (Tor tambroides); Nile tilapia (Oreochromis niloticus); European sea bass (Dicentrarchus labrax); Zebrafish (Danio rerio); Kenyi cichlid (Maylandia lombardoi); Turbot* (Psetta maxima); Atlantic cod (Gadus morhua); Turbot (Scophthalmus maximus); Clownfish (Amphiprion percula); Rohu (Labeo rohita); Iced freshwater fish (Lates niloticus); Common carp (Cyprinus carpio); Brown trout (Salmo trutta); Atlantic salmon (Salmo salar); Yellow catfish (Pelteobagrus vachelli); Rotifer (Brachionus plicatilis); Grouper (Epinephelus coioides); Senegalese sole (Solea senegalensis); Lumpfish (Cyclopterus lumpus); Atlantic halibut (Hippoglossus hippoglossus); Sea bass (Dicentrarchus labrax).
[1] – discussed in the review of Newaj-Fyzul et al. (2014); [2] – discussed in the review of Hayatgheib et al. (2020); [3] – discussed in the review of De et al. (2014); [4] – discussed in the review of Irianto and Austin (2002a); [5] - discussed in the paper of Tapia-Paniagua et al. (2012); [6] – discussed in the review of Cámara-Ruiz et al. (2020).

significantly improved survival (87.0%) compared with the control (54.6%) after infection with live *A. hydrophila*. An *Alcaligenes* sp. at inclusion level of 10^8 CFU g^{-1} feed, was fed to Malaysian Mahseer (*Tor tambroides*) for 90 days (Asaduzzaman et al., 2018). Weight gain, gut histology (villi height, villi with and villi area), and production of short chain fatty acids (SCFAs) significantly improved, and modulation of the gut microbiota Wang et al. (2020a) conducted a three-month feeding trial with Nile tilapia (*Oreochromis niloticus*) to determine the effect of *Alcaligenes faecalis* Y311 supplementation and revealed increase of alkaline phosphatase activities in gill and intestine. Probiotic administration did not affect the dominant bacteria but affected the relative abundance of some low abundance bacteria, *Methyloparacoccus*, *Enterococcus*, *Limnohabitans*, *Tepidimonas* and *Cetobacterium* in skin, gill and intestine. One interesting finding was that the relative abundance of *Acinetobacter*, potential pathogen, decreased in the gut by *A. faecalis* Y311 administration.

Alteromonas

Genus *Alteromonas* are facultative anaerobic bacteria, and in the absence of oxygen, the genus possess capabilities to use of a variety of other electron acceptors for respiration, for example trimethylamineoxide (Ringø et al., 1984). The genus is isolated from the GI tract of finfish (e.g., Akimoto et al., 1990; Jiang et al., 2018; Fonseca et al., 2019), and some information is available on the use of *Alteromonas* as probiotic supplement in shellfish (Ringø, 2020), but less information is available on their use as probiotics in finfish aquaculture (Mladineo et al., 2016). Mladineo et al. (2016) revealed improved phagocytic activity, respiratory burst, and gene expression of *lysozyme*, *Mx protein*, *caspase 3*, *TNF-a*, and *IL-10*, by *Alteromonas* sp. administrated to European sea bass (*Dicentrarchus labrax*).

Chromobacterium

Chromobacterium is a facultative anaerobic, motile and non-sporing coccobacillus, present in the GI tract of finfish (Ziólkowska et al., 2009; Zhou et al., 2016).

In a recent study, Yi et al. (2019) evaluated the effect of administration of a *Chromobacterium aquaticum* isolated from lake water with bacteriocin-like activity on zebrafish (*Danio rerio*) and revealed improved hepatic mRNA expression of carbohydrate metabolism-related genes, including glucokinase, hexokinase, glucose-6-phosphatase and pyruvate kinase, and growth-related genes, induced effect on innate immune-related genes and enhanced resistance against *A. hydrophila* and *Streptococcus iniae* by probiotic administration.

Enterobacter

Genus *Enterobacter* is rod shaped, facultative anaerobic, non-spore-forming bacteria and belong to family Enterobacteriaceae. During the last years, information has become available showing the presence of *Enterobacter* in intestine of finfish (e.g., Tapia-Paniagua et al., 2014a; Tapia-Paniagua et al., 2019; Terova et al., 2019; Nguyen et al., 2020).

Burbank et al. (2011) reported administration of *Enterobacter* strain PIC15 and *Enterobacter amnigenus* to rainbow trout for 7 days and revealed significant improved resistance against *Flavobacterium psychrophilum*. Furthermore, as both probiotic strains were isolated from the GI tract, this finding may indicate their ability to colonize the GI tract. Kenyi cichlid (*Maylandia lombardoi*) fed 60 days on an *Enterobacter cloacae* isolated from curd revealed enhanced growth, respiratory burst activity, and modulated the gut microbiota (Girijakumari et al., 2018). Moreover, it is of interest to notice that dietary administration of *Enterobacter cloacae* in combination with *Bacillus mojavensis* at 10^8 CFU g^{-1} to rainbow trout for 60 days improved protection against *Y. ruckeri*, as survival rate increased to 99.2% *vs*. 35% in the control group (Capkin and Altinok, 2009).

Phaeobacter

Genus *Phaeobacter* belongs to family Rhodobacteraceae and was first suggested by Martens et al. (2006). *Phaeobacter* is important as a carbon and sulfur metabolizer, and a biofilm former and antibiotic tropodithietic acid producer (TDA) a sulfur-containing compound (Porsby et al., 2008; Dittmann et al., 2020). Most of the cultured strains of *Phaeobacter* are isolated from aquatic environments, and from the intestine of finfish (Hjelm et al., 2004; Planas et al., 2004; Terova et al., 2019). Information is available on its use as probiotic, as well as a part of

multi strains probiotics supplementation with *Bacillus pumilus* (Schmidt et al., 2017), and *Phaeobacter inhibens* in combination with vibriophage KVP40 (Rasmussen et al., 2019).

In a previous review, Dimitroglou et al. (2011) discussed probiotic administration of *Phaeobacter* in Mediterranean finfish, and in order to avoid overlaps we recommend readers with interest to have a closer look at the papers discussed in the above mention review.

Phaeobacter gallaeciensis isolated from seawater of scallop cultures and administrated to Atlantic cod (*Gadus morhua*) larvae enhanced survival towards *Vibrio anguillarum* serotype 01 (D'Alvise et al., 2012). In a later study with Atlantic cod larvae, improved resistance against *V. anguillarum* 02α was noticed when *Phaeobacter* sp. isolated from turbot hatchery was added into well dishes at 10^7 CFU mL^{-1} (D'Alvise et al., 2013). Based on their results, the author suggested that *Phaeobacter* was a promising probiont in marine larval culture, and that TDA contribute to its probiotic effect as a mutant of *P. gallaeciensis* did not reduce *V. anguillarum* numbers.

Planas et al. (2004) revealed that *Phaeobacter* 27-4 administration improved survival against *V. anguillarum* and detected 27-4 in GI lumen of turbot (*Scophthalmus maximus*) when the probiont was administrated to the larvae incorporated in rotifers, but 27-4 did not colonize the larval gut and intestinal epithelium.

A *Phaeobacter* strain isolated from turbot hatchery, grown on ceramic biofilter (probiofilter) revealed resistance against *V. anguillarum*, improved seawater quality by decreasing turbidity, but the bacterial diversity in larval turbot (*Psetta maxima*) gut was unchanged (Prol-García and Pintado, 2013). In a recent study, Dittmann et al. (2020) studied administration of a TDA producing *P. inhibens* strain DSM17395 isolated from mariculture environment to turbot larvae, and observed no effect on gut community structure, even though the relative abundance of Rhodobacterales in the GI tract decreased.

Pseudoalteromonas

Gauthier et al. (1995) proposed that genus *Pseudoalteromonas*, aerobic, non-spore forming rods was split from *Alteromonas*. They produce a broad range of anti-bacterial products (Jin et al., 2010; Offret et al., 2016; Richards et al., 2017), and are reported in finfish intestine (e.g., Fjellheim et al., 2007; Ringø et al., 2008; Jiang et al., 2018), as probiotics (Mladineo et al., 2016), and as a part of a multi-strain probiotic preparations with *Microbacterium*, *Ruegeria* and *Vibrio* fed to Atlantic cod larvae (Skjermo et al., 2015).

In a study using *Pseudoalteromonas* sp. Administrated to European sea bass (*Dicentrarchus labrax*), Mladineo et al. (2016) documented best stimulation of phagocytic activity, respiratory burst, and gene expression of *lysozyme*, *Mx protein*, *caspase 3*, *TNF-a*, and *IL-10*, by *Pseudoalteromonas* compared to *Alteromonas* sp. And *Enterovibrio coralii* administration.

Pseudomonas

Genus *Pseudomonas* belong to family Pseudomonadaceae, are rod-shaped, aerobic, catalase- and oxidase positive and contain approximately 200 species. The genus has a great metabolic diversity (Palleroni, 1992; Silby et al., 2011), and produce exopolysaccharides, which could make it difficult for pseudomonads to be phagocytosed by mammalian white blood cells and contribute to surface-colonizing biofilms that are difficult to remove from food preparation surfaces (Royan et al., 1999).

Several studies have revealed the probiotic potential of *Pseudomonas* (e.g., Giri et al., 2011; Giri et al., 2015; Giri et al., 2016), and they are able to colonize a wide range of niches, including the GI tract of finfish (e.g., Ringø et al., 1997; Ringø et al., 2006a; Navarrete et al., 2013; Wang et al., 2020a).

Genus *Pseudomonas* is frequently used in finfish aquaculture, and in order to avoid overlaps, previous studies discussed in the review of De et al. (2014); Hayatgheib et al. (2020) and Irianto and Austin (2002a) are only briefly presented in **Table 1**. Siderophore-producing *Pseudomonads* strains have successfully been applied as biocontrol agens to finfish. In an early study, Smith and Davey (1993) showed that the fluorescent pseudomonad F19/3 isolated from Atlantic salmonatlantic salmon (*Salmo salar*) with furunculosis inhibitied *in vitro* growth of *A. salmonicida* in culture media, and improved resistance of presmolts of brown trout (*Salmo trutta*) against *A. salmonicida* and the authors suggested that this finding was due to that the strain inhibited the pathogen by competing for free iron. Similarly, *Pseudomonas fuorecens* was regarded as effective probiont for rainbow trout conferring protection against *V. anguillarum* (Gram et al., 1999), but the strain did not protect Atlantic salmon against *A. salmonicida* despite that *in vitro* inhibition was revealed (Gram et al., 2001). (Korkea-aho et al. (2012) revealed that *Pseudomonas* sp. M162 administrated to rainbow trout fry colonised the GI tract, improved immunity and protection against *F. psychrophilum*, while administration of *P. fluorescens* at a inclusion level of 10^7 displayed enhanced growth rate, and feed conversion ratio of African catfish (*Clarias gariepinus*) (Osungbemiro et al., 2018). Haematological analyses of African catfish fed the *P. fluorescens* diets had significantly higher white blood cell than control diet. In addition, lower mortality rate and several intestine histopathological alterations were revealed in catfish fed diets supplemented with *P. fluorescens*. In two recent studies, González-Palacios et al. (2019; 2020) revealed that two *P. fluorescens* isolated from skin of trout could adhere to mucus, reduced adhesion of zoospores and cysts of *S. paracitica* in rainbow trout, stimulated phagocytic activity of macrophages, serum lysozyme activity and serum protein concentration, and might be promising for biocontrol of saprolegninosis. Giri et al. (2020) conducted a 8 weeks feeding trial with juvenile common carp to determine the effect of heat-killed *Pseudomonas aeruginosa* strain VSG2, and revealed enhanced lysozyme, protein level, and alkaline phosphatase. In serum and skin mucus, superoxide dismutase, glutathione, glutathione peroxidase, and myeloperoxidase levels significantly enhanced. Furthermore, mRNA expression of antioxidant genes significantly improved in liver. These positive effects were also noticed by improved resistance against *A. hydrophila*. Qi et al.

(2020) displayed that *Pseudomonas monteilii* JK-1 significantly inhibited *in vitro* growth of *A. hydrophila*, and based on this criterion administrated the bacteria to grass carp, and showed that the bacteria was not toxic to the fish, and improved resistance against *A. hydrophila*. According to Fu et al. (2017), administration of *Pseudomonas stutzeri* F11 to grass carp reduced the levels of ammonia-N, nitrite-N, and total N in the water over an extended range, but administration did not had any effect on nitrate-N level. Modulation of the water microbial community was observed, by increasing the relative abundance of *Bacteroidetes* and *Firmicutes*, in contrast to *Proteobacteria*, *Actinobacteria* and *Verrucomicrobia* which decreased.

P. aeruginosa strain VSG2 has also been used in a multi-strain probiotic preparation with *Bacillus subtilis* and *Lactobacillus plantarum* (Giri et al., 2015), revealing improved growth performance, immunity and disease resistance in rohu.

Psychrobacter

Genus *Psychrobacter* belongs to the family Moraxellaceae, are Gram-negative aerobic, oxidase-negative, catalase-positive, non-pigmented and non-motile coccoid bacteria. Information is available showing the presence of *Psychrobacter* in intestine of finfish (e.g., Bakke-McKellep et al., 2007; Ringø et al., 2006a; Ringø et al., 2016b), and some *Psychrobacter* strains have successfully been used as probiotics to finfish (Sun et al., 2011; Sun et al., 2014; Makled et al., 2017; Makled et al., 2020).

Sun et al. (2011) administrated *Psychrobacter* sp. SE6 to grouper (*Epinephelus coioides*) and revealed only improvement in feed conversion ratio and serum component 4, while no effect was noticed on weight gain, specific growth rate (SGR), hepatopancreatic protease and lipase activity, intestinal amylase activity, and serum lysozyme - and superoxide dismutase activity, and serum component 3. In a later study, Sun et al. (2014) revealed that viable SE6 administration upregulated expression of TRL2 and TRL5 and cytokines, while results of heat-inactivated SE6 administration revealed that the MyD88-independent TLR2 signaling pathway was involved in the recognition of SE6. Use of *Psychrobacter namhaensis* administrated to Nile tilapia for 50 days, showed improved growth rate and feed utilisation ratio, haematocrit-, haemoglobin-, erythrocytes- and total leucocytes values by 2.8 x 10^7 CFU mL^{-1} supplementation *vs.* control fish (Makled et al., 2017). Moreover, immunoglobulin, alternative hemolysis, phagocytic and lysozyme activities significantly increased by feeding similar administration level. In a later study by the same authors, Makled et al. (2020) used *Psychrobacter maritimus* S, isolated from sediment as probiont to Nile tilapia. Growth rates, digestive enzymes (protease, lipase and amylase), phagocytic- and lysozyme activity, alternative complement hemolysis, hematological parameters significantly increased by 3.3 x 10^8 CFU mL^{-1} feeding, but slightly decreased at the highest inclusion level. Similarly, expression of interleukin-4 and 12 genes was significantly up-regulated by 3.3 x 10^8 CFU mL^{-1} feeding, while heat shock protein gene was down-regulated. Based on their results, the authors concluded that *P. maritimus* S at inclusion level of 3.3 x 10^8 CFU mL^{-1} is a promising probiont for Nile tilapia fingerlings.

Even though some information is available on *Psychrobacter* as probiotic in finfish, the genus deserves more attention as findings indicate that *Psychrobacter* might be capable of producing and secrete antimicrobial compounds (Wanka et al., 2018).

Rhodopseudomonas palustris

Rhodopseudomonas palustris is a rod-shaped photosynthetic bacterium, with an ability to switch between four different modes of metabolism. The bacterium has been isolated from swine waste lagoons, earthworm droppings, marine coastal sediments, sludge for use in a recirculating aquaculture system (Kim et al., 1999), pond water (Wang, 2011; Zhang et al., 2014), used in fluidizes bed biofilters (Zhan and Liu, 2013), and in some probiotic studies (Zhou et al., 2010; Wang, 2011; Zhang et al., 2014; Liu et al., 2020).

Zhou et al. (2010) revealed that administration during 40 days of a diet supplemented with *R. palustris* GO6 increased significantly the tilapia growth performance, respiratory burst-, superoxide dismutase-, catalase- and myeloperoxidase activities, while no effect was revealed regarding total serum protein, albumin, globulin, serum lysozyme content. In this study, administration of two bacilli species were included, and the author's conclusion was *Bacillus coagulans*, followed by G06 were better water additives than *B. subtilis* to tilapia. In a 60-day study with grass carp, Wang (2011) reported that *R. palustris* administration enhanced growth performance and amylase activity in proximal intestine (PI) and distal intestine (DI), while protease- and cellulase activities in PI and DI were not affected. Although *R. palustris* supplementation revealed some positive effect, the best results were revealed by *Bacillus coagulans*. Zhang et al. (2014) demonstrated that *R. palustris* administration to grass carp culture significantly decreased ammonia-N, total inorganic-N and total-N in water, and modulated the water microbiota, by affecting the relative abundance of Proteobacteria, Bacteroides and Actinobacteria. In a study with yellow catfish (*Pelteobagrus vachelli*), Liu et al. (2020) revealed that *R. palustris* in effluent increased protease-, amylase-, and lipase activities, and alkaline phosphatase, acid phosphatase, superoxide dismutase and catalase by up-regulating gene expression. Furthermore, disease resistance towards *A. hydrophila*, and modulation of the gut microbiota was observed by significantly increased the relative abundance of bifidobacteria and lactobacilli.

Roseobacter

Roseobacter species have been identified as both oval and rod-like shaped motile cells, are marine species and have a major role in oceanic sulfur cycling (Buchan and Moran, 2005; Wagner-Döbler and Biebl, 2006). They are heterotrophs, anaerobic and possess N-acyl homoserine lactones (AHLs) based quorum sensing systems (Tang et al., 2010; Cude and Buchan, 2013). During the last years, information has become available showing the presence of *Roseobacter* in intestine of finfish (e.g., Hjelm et al., 2004; Fjellheim et al., 2007).

Roseobacter species as candidate probiotic bacteria of the fish could antagonize fish-pathogenic bacteria without harming the fish or their live feed. Makridis et al. (2005; 2008) revealed similar survival of gilthead sea bream larvae exposed to 6 x 10^5 *Roseobacter* mL^{-1} when larvae were reared in sterile seawater, while lower survival was noticed when larvae were held in filtered seawater. spp. sp.

Roseobacter species revealing antagonism against *Vibrio* species in combination with algae could be a possible probiotic organism in larval rearing.

Shewanella

The genus is included in family Shewanellaceae, is facultative anaerobic in the absence of oxygen, and members of the genus have capabilities to use of a variety of electron acceptors for respiration. Most of the bacteria in the genus are revealed in extreme aquatic habitats, at low temperature, and at high pressure. *Shewanella* are a normal component of the surface microbiota of several finfish species (e.g., Satomi et al., 2006; Fjellheim et al., 2007; Satomi et al., 2007; Navarrete et al., 2013; Egerton et al., 2018).

Genus *Shewanella* is one of the most frequently used Gram-negative probiotics in finfish aquaculture, as the bacterium inhibit *in vitro* growth of *Photobacterium damselae* subsp. *piscicida*, *Vibrio harveyi*, *Vibrio alginolyticus* and *V. anguillarum* (Chabrillón et al., 2005a; Chabrillón et al., 2005b; Chabrillón et al., 2006).

Within genus *Shewanella*, is *Shewanella putrefaciens* Pdp11 most frequently used. Guzmán-Villanueva et al. (2014) used Pdp11 as a probiotic supplementation to gilthead seabream (14.5 g) in a 4-week study, and revealed significant lower serum IgM levels, and serum peroxidase activity after 4 weeks, while growth performance (SGR and condition factor), serum antiprotease -, leucocyte peroxidase- serum antiprotease and leucocyte peroxidase activities were unaffected by probiotic feeding compared to control fed fish. In two studies using enriched of *Artemia* by *S. putrefaciens* Pdp11 to Senegalese sole (*Solea senegalensis*) larvae, Lobo et al. (2014a; 2014b), revealed improved growth and modulation of the gut microbiota. In a later study, Lobo et al. (2016) showed that *Artemia* metanauplii used as live vector for Pdp11 administration, improved growth of the sole and affected lipid profile.

In a recent study, Chen et al. (2020b) revealed that administration of Pdp11 facilitated wound closure, and increased the albumin/globulin ratio, protease and peroxidase activities in skin mucus, 7 days after post-wounding, but decreased serum aspartate aminotransferase. In addition, probiotic administration up-regulated gene expression of antioxidant enzymes and anti-inflammatory cytokines (*il-10* and *tgf- β*) but decreases pro-inflammatory cytokines (*il-1 β, il-6, il-8* and *tnf-α*). Based on their results, the authors concluded that Pdp11 had a positive effect on wound healing and skin damage. This conclusion was strengthened by Chen et al. (2020c) evaluating administration of Pdp11 on gene expression of the intestinal inflammatory response and barrier function of gilthead seabream.

An interesting approach regarding probiotics, using *Shewanella* sp. MR-7 isolated from turbot intestine that could utilize soybean meal (SBM) in turbot intestine was evaluated by Li et al. (2019b). SBM fermented by the bacterium and fed to turbot counteracted inflammatory response and modulated mucosal microbiota at both phylum and genus level, but no significant effect was noticed on trypsin, diastase (catalyze the breakdown of starch into maltose) and lipase activities. These interesting findings merit further investigations by including disease-, immunological- and gene expression studies.

S. putrefaciens Pdp11 is also used in combination with *Bacillus* sp. and palm fruits extracts in a study evaluated antioxidant enzyme gene expression in the mucus of gilthead seabream (*Sparus aurata* L.) (Esteban et al., 2014).

According to Seoane et al. (2019), *S. putrefaciens* Pdp11, presents features that can explain its probiotic benefits; specific proteins for adhesion and colonization of the GI tract, resistance to bile salt, and inhibition of pathogen adhesion in the gut.

A dietary supplementation of *Shewanella xiamenensis* A-1 and A-2 isolated from grass carp was administrated to grass carp for 28 days and thereafter challenged with *A. hydrophila* (Wu et al., 2015). A significant enhancement of respiratory burst, and phagocytic and lysozyme activities, and upregulation of immune related genes (*IL-8, IL-1β, lysozyme-C* and *TNF-α*), and resistance against *A. hydrophila* were revealed. In later study, Hao et al. (2017) supplemented grass carp diet with a dose of 10^8 CFU g^{-1} of *S. xiamenensis* for 28 days, and at the end of feeding modulation of the gut microbiota was noticed. The relative abundance of *Meganema* and *Rubellimicrobium* increased, *Lactococcus*, *Pseudomonas* and *Citrobacter* (cellulose degrading bacteria) decreased, while *Flavobacterium* was not detected compared to control fed fish.

Asaduzzaman et al. (2018) revealed that administration of *Shewanella* sp. to Malaysian Mahseer for 90 days, improved gut histology (villi height, villi with and villi area), gut production of SCFAs, and modulated the gut microbiota. In a more recent study, administration of *Shewanella* sp. MR-7 to turbot, ameliorate lipopolysaccharide induced intestinal dysfunction (villus and microvilli height), and modulated the gut microbiota by enhancing the relative abundance of *Lactobacillus*, and reducing the relative abundance of *Pseudomonas* (Zhang et al., 2020).

Aliivibrio

The taxonomy and phylogeny of genus *Photobacterium* is revised, for example, *Photobacterium logei* and *Photobacterium fischeri* are now considered members of genus *Aliivibrio* (Labella et al., 2017). *Aliivibrio* is reported in the intestinal tracts of vertebrates as well as finfish (Green et al., 2013; Karlsen et al., 2017; Rud et al., 2017; Hamilton et al., 2019), and some information is available on their use as probiotics in finfish aquaculture.

Vibrio viscosus reclassified as *Moritella viscosa* (Benediktsdottir et al., 2000) is a bacteria species associated with "*winter ulcer*", affecting salmonids reared in seawater. In two recent studies, Klakegg et al. (2020a; 2020b) investigated the effect of *Aliivibrio* strains isolated from the mandibulum of

farmed Atlantic salmon on growth performance and ulcer prevalence of Atlantic salmon, and ulcer prevalence of lumpfish (*Cyclopterus lumpus*), respectively. Both studies, revealed improved growth performance and ulcer prevalence after adding *Aliivibrio* into the tank water. Based on their results, the author suggested that *Aliivibrio* administration may have impact on welfare, economy and sustainability in aquaculture as fewer ulcer outbreak caused by *M. viscosa* was noticed.

Enterovibrio

In a study evaluating *Enterovibrio coralii* administration to European sea bass (*Dicentrarchus labrax*), Mladineo et al. (2016) revealed no significant stimulation of phagocytic activity, respiratory burst, and gene expression of *lysozyme*, *Mx protein*, *caspase 3*, *TNF-a*, and *IL-10*.

Vibrio

Genus *Vibrio* has a curved-rod (comma) shape, are reported in salt water, and are facultative anaerobe and oxidase positive bacteria. Even through several species of *Vibrio* are among the most common bacteria leading to massive mortality of cultured fish, and shellfish (Ina-Salwany et al., 2019), several studies have reported that *Vibrio* is dominant in the GI tract of fish (e.g., Eddy and Jones, 2002; Fonseca et al., 2019). Even though genus *Vibrio* are pathogenic, several studies have used apathogenic *Vibrio* as probiotic in finfish aquaculture (Austin et al., 1995; Gatesoupe, 1997; Ringø and Vadstein, 1998; DeSchrijver and Ollevier, 2000; Ottesen and Olafsen, 2000; Makridis et al., 2001; Aerts et al., 2018; Schaeck et al., 2016), as well as a part in a multi-strain probiotic supplementation with *Microbacterium*, *Ruegeria* and *Pseudoalteromonas* (Skjermo et al., 2015), and in combination with *A. veronii* and *Flavobacterium sasangense* (Chi et al., 2014).

In an early study, Ottesen and Olafsen (2000) evaluated the effect of water administration of *Vibrio iliopiscarius* and apathogenic *Vibrio salmonicida* on Atlantic halibut (*Hippoglossus hippoglossus*) larval survival. Pre-incubation of larvae with apathogenic *V. salmonicida* improved survival to 94.4%, whereas *V. iliopiscarius* administration reduced survival to 63% compared to 81% survival in the control group.

Makridis et al. (2001) reported the use of *Vibrio* strain PB 1-11 and strain PB 6-1 encapsulated in *Artemia franciscana* and revealed that total CFU in water was lower by encapsulation, while larval gut microbiota was not significantly affected by encapsulation. Schaeck et al. (2016) used a *Vibrio lentus* as probiotic supplement in a study with gnotobiotic European sea bass (*Dicentrarchus labrax*) larvae, and displayed improved resistance against *V. harveyi*, but administration of *Vibrio proteolyticus* did not revealed any effect on larval survival. In a following study, Schaeck et al. (2017) revealed that *V. lentus* administration to gnotobiotic European sea bass larvae significantly modified gene expression did not affect apoptotic and cell proliferative indexes. Aerts et al. (2018) evaluate the probiotic potential of *V. lentus*, as inoculum into well water containing gnotobiotic European sea bass larvae at day 8 post hatching, and revealed significantly decreased glucocorticoid baseline levels in larvae, and the authors suggested that their findings provided a better insight into the hypothalamic-pituitary-interrenal axis. Furthermore, *Vibrio* species, such as *Vibrio natriegens* which show high capacity to hydrolyze casein, could increase feed efficiency and improve the growth rate of fish (Rahman et al., 2016).

GRAM-POSITIVES

The beneficial effects of Gram-positive probiotic bacteria used in finfish aquaculture, and studies discussed in the review of De et al. (2014); Hayatgheib et al. (2020); Tran et al. (2020) and van Doan et al. (2021) are only briefly presented in **Table 2**.

Arthrobacter

Genus *Arthrobacter*, has no spores and capsule, utilizes a wide and diverse range of organic substances, and has ability to produce antimicrobial compounds (O'Brien et al., 2004; Papaleo et al., 2012). They are reported in finfish intestine (e.g., Ringø et al., 2006a; Ringø et al., 2008; Nayak, 2010; Wang et al., 2019b), but less information is available on their use as probiotic to finfish (Lauzon et al., 2010). Some information is available on its use in a multi-strain probiotic mixture (Geng et al., 2012a; Peixoto et al., 2018).

An *Arthrobacter* sp. strain that showed inhibitory potential against fish pathogens *in vitro* was used in a bath treatment of Atlantic cod larvae (Lauzon et al., 2010), and regularly administration to the rearing water, revealed that the bacterium could establish in the larval intestine.

Bifidobacterium

Numerous health benefits have been claimed for genus *Bifidobacterium*, the "*good bacteria*". Compared to *Lactobacillus acidophilus*, are bifidobacteria less acid tolerant as they do not grow below pH 5.0 (Shah, 1997), while *Lb. acidophilus* grow below 4.0. *Bifidobacterium* are reported in the GI tract of finfish (Vlkova et al., 2012; Piazzon et al., 2019; Wang et al., 2020b), but *Bifidobacterium* is less incorporated into diets or added to the rearing water in finfish aquaculture (Sahandi et al., 2017; Sahandi et al., 2019). In addition, *Bifidobacterium bifidium* was administrated to Siberian sturgeon (*Acipenser baerii*) in combination with *Lactobacillus* spp. and *B. subtilis*, and the results revealed improved growth performance, hematological and immune parameters (Hassani et al., 2020).

In two studies with rainbow trout, Sahandi et al. (2017; 2019) used two bifidobacteria, *Bifidobacterium animalis* PTCC-1631 and *Bifidobacterium animalis* subsp. *lactis* PTCC-1736, isolated from rat feces and fermented milk, respectively, and administration of 10^7 CFU g^{-1}, revealed positive effect on growth, nutrient utilization, digestibility, feed conversion ratio, red and white blood cell content, serum biochemical and reduction of cortisol level of rainbow trout.

in vitro Brochothrix

Genus *Brochothrix* is non-spore-forming, non-motile catalase-positive, facultative anaerobic, rod-shaped bacteria that show characteristic changes in cell morphology during growth. Sneath and Jones (1976) proposed the genus for some meat spoilage

TABLE 2 | Effect of Gram-positive bacteria on growth performance, gut health, immune system and disease resistance in finfish, and an *in vitro* study.

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
Arthrobacter sp.	Atlantic cod larval rearing water	10^{10} CFU mL^{-1}, added regularly to the rearing water, 38 days	Atlantic cod larvae	Can establish in larval GI tract	Lauzon et al. (2010)
Bifidobacterium animalis PTCC-1631 and *Bifidobacterium animalis* subsp. *lactis* PTCC-1736	PTCC-1631 rat feces and PTCC-1736 fermented milk	10^7, $2x10^7$, $3x10^7$, CFU g^{-1}, 60 days	Rainbow trout ~ 0.6 g	↑ growth, red and white blood cell content, serum biochemical ↓ reduction of cortisol level	Sahandi et al. (2017)
B. animalis PTCC-1631 and *B. animalis* subsp. *lactis* PTCC-1736	PTCC-1631 rat feces and PTCC-1736 fermented milk	10^7 (T_1) $2x10^7$, $3x10^7$, CFU g^{-1}, 8 weeks	Rainbow trout ~ 0.6 g	↑ growth, nutrient utilization, digestibility (T_1) ↓ feed conversion ratio (T_1)	Sahandi et al. (2019)
Brochothrix thermosphacta	Unknown, laboratory strain	10^{10} CFU g^{-1}, 14 days	Rainbow trout ~ 25 g	↑ respiratory burst activity and resistance against *Aeromonas bestiarum*, a bacterium cause skin infection	Pieters et al. (2008)[1]
Clostridium autoethanogenum	Single cell protein of *C. autoethanogenum*	Inclusion level, 0, 4.85, 9.7, 14.55, 19.4, 38.8, and 58.2% replacement of fish meal (FM)	Black sea bream ~ 6 g	→ growth performance, antioxidation and digestive enzyme activities ↓ total superoxide dismutase in serum of fish fed the highest inclusion level	Chen et al. (2019a)
C. autoethanogenum	Single cell protein of *C. autoethanogenum*	Inclusion level, 0, 25, 50 and 75% replacement of FM	Largemouth bass ~ 15 g	With increasing inclusion level, ↓ the total antioxidant capacity of liver, ↑ plasma phosphatase activity	Lu et al. (2021)
C. autoethanogenum	Single cell protein of *C. autoethanogenum*	Inclusion level, 0, 50, 100, 150 and 200 g kg^{-1} replacement of soybean meal	GIFT; Nile tilapia ~ 0.7 g	Affected whole-body crude protein, plasma triglycerides, upregulated mRNA expression of growth-related insulin growth factor (IGF-1), intestinal absorption, antioxidant status and immune response	Maulu et al. (2021a; 2021b)
C. butyricum	Commercial strain	300 μg kg $fish^{-1}$, 3 days	Rainbow trout, 10 or 50 g	↑ resistance against *V. anguillarum*	Sakai et al. (1995)[2]
C. butyricum	Isolated from chickens	10^4, 10^5, 10^7, 10^9 CFU g^{-1}, 8 weeks	Chinese drum, 200 – 260 g	↑ growth and humoral immune responses	Song et al. (2006)[2]
C. butyricum CB2	Isolated from chickens	10^8 CFU g^{-1}, 30 days	Chinese drum, 200 -260 g	↑ resistance against *V. anguillarum* and *Aeromonas hydrophila*, and immune responses	Pan et al. (2008)[1,2]
C. butyricum MIYAIRI II588	Commercial strain	*In vitro* study using intestinal epithelial cells	Epithelial cells crucian carp	Prevented and treated *Salmonella enteritidis* and *Vibrio parahaemolyticus* infections	Gao et al. (2013)[2]
C. butyricum MIYAIRI II588	Commercial strain		Silver pomfret ~ 5.3 g	↑ growth, digestive- and innate immunity enzymes → feed conversion ratio and survival	Gao et al. (2016)[2]
C. butyricum CBG01	Unknown, laboratory strain	10^9 CFU g^{-1}, 60 days	Hybrid grouper ~ 44 g	↑ serum superoxide activity → growth performance, digestive and non-specific immune enzymes activities	He et al. (2017)[2]
C. butyricum	Unknown, laboratory strain	10^4, 10^5, 10^6, 10^7 CFU g^{-1}, 56 days	Tilapia ~ 56.2 g	Suitable dose enhance growth performance, elevated humoral and intestinal immunity, modulated the diversity of the intestinal microbiota, by increasing *Bacillus*, while relative abundance of *Aeromonas*, *Cetobacterium* and Gamma-proteobacteria decreased ↑ resistance against *Streptococcus agalactiae*	Li et al. (2019c)[2]
C. butyricum	Fish diet	10^4 CFU g^{-1} and 10^6 CFU L^{-1}, 56 days	Gibel carp ~ 5 g	↑ immune responses and survival against *Carassius auratus* herpesvirus	Li et al. (2019d)[2]
C. butyricum	Commercial	1, 2, 4 and 8 g kg^{-1} of 1.5 x 10^8 CFU g^{-1}, 8 weeks	Tilapia ~ 14 g	↑ weight gain, apparent digestibility coefficient, villus height in anterior intestine, resistance against *A. hydrophila* ↓ feed conversion ratio, numbers of *Escherichia coli*	Poolsawat et al. (2020)[2]
C. butyricum	Unknown, laboratory strain	$3x10^{10}$, $1.5x10^{11}$ and $3x10^{11}$ CFU kg^{-1}, 90 days	Tilapia ~ 3.2 g	↑ growth performance, amylase, lipase and trypsin activities at $1.5x10^{11}$ CFU kg^{-1}, antioxidant capacity Modulation of the gut microbiota, functions related to nitrogen metabolism, phosphorylation and proteinases	Zhang et al. (2020)
C. butyricum	Unknown, laboratory strain	$0.25x10^7$ and 10^7 CFU g^{-1}, 8 weeks	Common carp ~ 90 g	↑ intestinal enzyme activity, short chain fatty acids, intestinal gene expression, intestinal histology and diversity of intestinal microbiota → growth performance	Meng et al. (2021)

(Continued)

TABLE 2 | Continued

Species	Isolated from	Doses and duration	Finfish species investigated	Parameters investigated	References
Kocuria AP4	Clownfish	10^5 mL^{-1}	Clownfish larvae	↑ survival	Vine (2004)
Kocuria sp. SM1	Rainbow trout intestine	10^8 CFU g^{-1}, 2 weeks	Rainbow trout, 10-15 g	↑ resistance against *V. anguillarum* and *Vibrio ordalli*	Sharifuzzaman and Austin (2010b)[3,4]
Kocuria sp. SM1	Rainbow trout intestine	0.1 mL of 2.0 ± 0.5 mg mL^{-1} ECPs, CWPs and WCPs fish^{-1}, 7 days	Rainbow trout, 10-15 g	↑ resistance against *V. anguillarum*	Sharifuzzaman et al. (2011)[4]
Kocuria sp. SM1	Rainbow trout intestine	~ 10^8 CFU g^{-1}, 14 days	Rainbow trout ~ 15 g	↑ in epidermal mucus and goblet cells in hindgut → growth performance, gut histology in pyloric caeca and foregut, digestive enzymes activity (API ZYM test), and serum biochemical parameters ↓ in vacuole-containing enterocytes	Sharifuzzaman et al. (2014)
Microbacterium	Atlantic cod larvae	$10^4$and 10^7 mL^{-1} in wells	Atlantic cod larvae	↑ resistance against *V. anguillarum* 02a	Fjellheim et al. (2010)
Micrococcus MCCB 104	Unknown, laboratory strain	10^3 CFU animals^{-1} day^{-1}, 28 days	Pearl spot and tilapia, equal size (length 5-6 cm and 60-70 days old)	Affected digestive enzyme activities in both fish species	Sankar et al. (2017)
Micrococcus luteus A1-6	Fish intestine, no specification	10^6 – 10^8 cells g^{-1}, 56 days	Rainbow trout ~ 9 g	↑ resistance against *A. salmonicida*, lysozyme activity and macrophages in kidney → numbers of erythrocytes and leucocytes	Irianto and Austin (2002b)[1,4]
M. luteus	NI	10^7 CFU g^{-1}, 90 days	Nile tilapia ~ 21 g	↑ resistance against *A. hydrophila* → growth performance, and hemato-logical and biochemical parameters	Abd El-Rhman (2009)[3,4]
Paenibacillus ehimensis	Water of tilapia culture pond	10^6 and 10^7 CFU g^{-1}, 2 months	Nile tilapia ~ 5.6 g	↑ growth performance, immune parameters, and resistance against *A. hydrophila* and *S. iniae*	Chen et al. (2019b)[1]
Paenibacillus polymyxa	Unknown, laboratory strain	10^9 CFU g^{-1}, 80 days	Common carp fry ~ 0.33 g	↑ growth performance, non-specific innate immune parameters, and resistance against *A. hydrophila*	Gupta et al. (2014)
Paenibacillus polymyxa	Unknown, laboratory strain	Added to tank water, 10^3, 10^4 and 10^5 CFU mL^{-1}, 8 weeks	Common carp ~ 32.2 g	↑ water quality, fish survival, innate immune response, and resistance against *A. hydrophila*	Gupta et al. (2016)
Rhodococcus SM2	Rainbow trout intestine	0.1 mL of 2.0 ± 0.5 mg mL^{-1} ECPs, CWPs and WCPs fish^{-1}, 7 days	Rainbow trout, 10-15 g	↑ resistance against *V. anguillarum*	Sharifuzzaman et al. (2011)
Rhodococcus SM2	Rainbow trout intestine	~ 10^7 CFU g^{-1}, 14 days	Rainbow trout ~ 15 g	↑ in epidermal mucus and goblet cells in hindgut → growth performance, gut histology in pyloric caeca and foregut, digestive enzymes activity (API ZYM test), and serum biochemical parameters ↓ in vacuole-containing enterocytes	Sharifuzzaman et al. (2014)[4]
Rhodococcus sp.	Skin mucus of brook charr	Added to tank water, twice a day at a concentration of 10^5 mL^{-1}	Brook charr 16 ± 5.8 g	The probiont did not colonize the skin mucus, but was detected in the biofilm of the tank ↓ population level of *Flavobacterium psychrophilum*	Boutin et al. (2013)

NI, no information given; GI tract, gastrointestinal tract. ↑ - increase; → no effect; ↓ - decrease.
Atlantic cod (Gadus morhua); Rainbow trout (Oncorhynchus mykiss); Sea bass (Dicentrarchus labrax); Black sea bream (Acanthopagrus schlegelli); Largemouth bass (Micropterus salmoides); Chinese drum (Miichtys miiuy); Crucian carp (Carassius carassius); Silver pomfret (Pampus argenteus); Hybrid grouper (Epinephelus lanceolatus ♂ X Epinephelus fuscoguttatus ♀); Nile tilapia (Oreochromis niloticus); Gibel carp (Carassius auratus gibelio); Nile tilapia (Oreochromis niloticus); Common carp (Cyprinus carpio); Clownfish (Amphiprion percula); Atlantic cod (Gadus morhua); Pearl spot (Etroplus suratensis); Brook charr (Salvelinus fontinalis).
[1] – discussed in the review of Hayatgheib et al. (2020); [2] – Tran et al. (2020); [3] – discussed in the review of De et al. (2014); [4] - discussed in the review of van Doan et al. (2021).

bacteria, previously designated as *Microbacterium thermosphactum*. The scientific interests have mostly focused on *Brochothrix thermosphacta* as the bacterium is associated with off-odour development in meats, especially in prepacked products held at refrigeration temperatures. They are isolated from the GI tract of finfish (Ringø et al., 2006a; Ringø et al., 2008; Higuera-Llanten et al., 2018), but less information is available on their use as probiotics in aquaculture (Pieters et al., 2008).

Administration of *B. thermosphacta* BA211 at 10^{10} g^{-1} in rainbow trout diet for 2 weeks increased fish survival against challenge with *Aeromonas bestiarum* (Pieters et al., 2008).

Clostridium

Genus *Clostridium* is a butyric-acid producer, and butyrate is the preferred energy source for the colon epithelial cells, contributes to the maintenance of the gut barrier functions, and has

immunomodulatory and anti-inflammatory properties (Riviere et al., 2016; Guo et al., 2020). *Clostridium* are isolated from finfish intestine (e.g., Wu et al., 2012; Abdelhamed et al., 2019; Pérez-Pascual et al., 2020; Rimoldi et al., 2020), and some strains are frequently used as probiotics to enhance growth and immune response in finfish (for review see Tran et al., 2020; **Table 2**) as well as in shellfish aquaculture (Ringø, 2020; Tran et al., 2020).

Single cell protein of *Clostridium autoethanogenum* has been evaluated in four recent studies (**Table 2**). Chen et al. (2019a) evaluated the effect of partial replacement of fish meal with *C. autoethanogenum* single-cell protein (CAP) fed to juvenile black sea bream (*Acanthopagrus schlegelli*) and revealed that dietary treatments did not significantly affect malondialdehyde, catalase, total antioxidant capacity and digestive protease, lipase and amylase activities. On the other hand, total superoxide dismutase in serum of fish fed the highest inclusion CAP level, 58.2%, was significantly lower than that of control fed fish.

An overview on the use of *C. butyricum* as probiotics was presented by Tran et al. (2020) and to avoid overlaps, the results discussed in the abovementioned review are only summarized in **Table 2**. He et al. (2017) noted no effect on growth performance, digestive enzyme activities, serum- lysozyme, catalase and glutathione peroxidase activities, but only improved serum superoxide activity by feeding hybrid grouper (*Epinephelus lanceolatus* ♂ x *Epinephelus fuscoguttatus* ♀) *C. butyricum*, at inclusion level of 10^9 CFU kg^{-1}, compared to fish fed only *Lb. acidophilus* or a combination with *Lb. acidophilus*, *Bacillus cereus* and *C. butyricum*. In a recent study, Meng et al. (2021) administrated a commercial *C. butyricum* at two inclusion levels; 0.25 x 10^7 (LVB) and 10^7 (HCB) CFU g^{-1}, for 8 weeks to address the effect on intestinal enzyme activity, SCFAs, intestinal gene expression and diversity of intestinal microbiota of common carp (*Cyprinus carpio*). A substantial beneficial effect was noticed, probiotic administration by HCB significantly enhanced intestinal catalase and lysozyme, positively affected mucin secretion and the height of microvilli, and intestinal gene expression of *IL-10*, *TLR-2*, *MyD-88*, *ZO-1* and *Occludin*. Butyric- and propionic acid content were elevated in both clostridia treatments. Furthermore, the intestinal content microbiota was affected, with improved abundance of Bacteroides and a significant decrease in Fusobacteria and Proteobacteria. Zhang et al. (2020) used a commercial *C. butyricum* strain, previously used in shellfish studies at three administration levels. The authors revealed that inclusion level of $1.5x10^{11}$ CFU kg^{-1}, improved growth performance, digestive enzymes (amylase, lipase and trypsin), and antioxidant capacity in spleen, head kidney and liver of tilapia. Furthermore, modulation of the gut microbiota, functions related to phosphorylation, proteinases, and nitrogen metabolism were noticed.

Kocuria

Kocuria was first reported by *Kocuria* is coccus shaped, and have rigid cell walls and are either aerobic or facultative anaerobic bacteria (Venkataramana et al., 2016), and has been isolated from the GI tract of finfish (e.g., Bakke-McKellep et al., 2007; Linh et al., 2018; Sharifuzzaman et al., 2018).

According to Vine (2004) *Kocuria* AP4 administrated to clownfish larvae, improved survival. Rainbow trout orally fed *Kocuria* SM1 (10^8 cells g^{-1}) originally isolated from GI tract of rainbow trout, has been administrated to rainbow trout in three studies (Sharifuzzaman and Austin, 2010a; Sharifuzzaman and Austin, 2010b; Sharifuzzaman et al., 2011). In a later study using *Kocuria* SM1, Sharifuzzaman et al. (2014) revealed increase in in epidermal mucus and goblet cells in hindgut, but growth performance, gut histology in pyloric caeca and foregut, serum biochemical parameters (hemoglobin, urea, creatinine and glucose), and digestive enzymes activity (API ZYM test) were not affected by probiotic feeding, while a notable decrease in vacuole-containing enterocytes was noticed. Furthermore, an interesting finding was that inflammation was not observed in fish fed *Kocuria* SM1. In most probiotic studies, the frequency of the probiont is evaluated after continuous feeding, but in the study of Sharifuzzaman et al. (2014) probiotic feeding by *Kocuria* SM1or *Rhodococcus* SM2 was stopped after 14 days and reverted back to the control diet for 14 days. The results of both probiotic bacteria revealed that percentage of the probiont in digesta reached maximum, at the end of day 14, but disappear upon switching to the control diet after 28 days. The authors concluded that this observation indicate no primary colonization in the GI tract, but to fully conclude the autochthonous microbiota should be analyzed.

Microbacterium

Genus *Microbacterium* belongs to the family *Microbacteriaceae* within suborder *Micrococcineae*. *Microbacterium* are non-spore-forming, rod-shaped bacteria, and was classified according to the amended genus description by Collins et al. (1983) and redefinition of Takeuchi and Hatano (1998). They are isolated from the GI tract of finfish (e.g., Ringø et al., 2006a; Ringø et al., 2006b; Hu et al., 2015), used as probiotics (Fjellheim et al. (2010), and in a multi-strain probiotic mixture with *Pseudoalteromonas*, *Ruegeria* and *Vibrio* fed to Atlantic cod larvae (Skjermo et al., 2015).

In a study to evaluate the selection of candidate probiotics, Fjellheim et al. (2010) revealed that *Microbacterium* sp. ID-3-10 improved survival of Atlantic cod larvae exposed to *V. anguillarum* 02a.

Micrococcus

Genus *Micrococcus* was divided into *Micrococcus, Kocuria, Nesterenkonia, Kytococcus* and *Dermacoccus* based on phylogenetic and chemotaxonomic studies by Stackebrandt et al. (1995). Information is available on their presence in finfish intestine (e.g., Ringø, 1993; Bakke-McKellep et al., 2007; Hu et al., 2015), and furthermore information is available on the potential of gut *Micrococcus* isolates as probiotics (e.g., Nurhidayu et al., 2012; Akayli and Urku, 2014; Akayli et al., 2016), and their use as probiotics in finfish aquaculture (Irianto and Austin, 2002b; Abd El-Rhman et al., 2009; Sankar et al., 2017).

Feeding *Micrococcus luteus* to rainbow trout and Nile tilapia, reduced mortality after challenged with *A. salmonicida* (Irianto and Austin, 2002b) and *A. hydrophila* Abd El-Rhman et al.

(2009). In a later study, Sankar et al. (2017) evaluated the effect of *Micrococcus* administration on digestive enzymes (pepsin, α-amylase, protease and lipase) activities, and revealed differences in pearl spot (*Etroplus suratensis*) and tilapia after 60 days feeding.

Paenibacillus

Previously, *Paenibacillus* species were included in genus *Bacillus* due to their common morphological and physiological characteristics. However, based on 16S rRNA gene sequences in 1993, *Paenibacillus* was reassigned as a new genus. Genus *Paenibacillus* has been isolated from humans, animals, plants as well as fish (Midhun et al., 2017; Ma et al., 2018; Wang et al., 2019c), but their use as probiotics in finfish aquaculture is less investigated.

Common carp fry administrated with *Paenibacillus polymyxa* improved growth performance, non-specific immune (lysozyme, respiratory burst and myeloperoxidase activities), and resistance against *A. hydrophila* (Gupta et al., 2014). Later the same authors (Gupta et al., 2016) revealed that *P. polymyxa* supplemented to the water at three concentrations, improved water quality, common carp survival, innate immune response (lysozyme, respiratory burst, myeloperoxidase, catalase and superoxide dismutase activities), and resistance against *A. hydrophila*, at 10^3 and 10^4 CFU mL^{-1} supplementation. In a recent study, Chen et al. (2019b) demonstrated that administration of *Paenibacillus ehimensis* enhanced growth performance, immune parameters, and resistance against *A. hydrophila* and *S. iniae*.

Rhodococcus

Genus *Rhodococcus* is aerobic, nonsporulating, non-motile bacteria closely related to *Mycobacterium* and *Corynebacterium*. Few species are pathogenic and *Rhodococcus* have been revealed in a broad range of environments, including soil and water, as well as fish intestine (Tapia-Paniagua et al., 2014a; Song et al., 2016; Sharifuzzaman et al., 2018). Strains of *Rhodococcus* is experimentally advantageous due to its relatively fast growth rate and simple developmental cycle.

In a study by Sharifuzzaman et al. (2011), the authors used paraprobiotic (cellular components) of *Rhodococcus* SM2 isolated from the intestine of rainbow trout and displayed enhanced trout immune response and a significant resistance to *V. anguillarum* challenge. In a subsequent study, Sharifuzzaman et al. (2014) revealed that administration with *Rhodococcus* SM2, ~ 10^7 CFU g^{-1} for 14 days, epidermal mucus and goblet cells in hindgut increased, while no significant effect was noticed on growth performance, gut histology in pyloric caeca and foregut, digestive enzymes activity, and serum biochemical parameters. Inflammation was not observed in fish fed *Rhodococcus* SM2.

In a study with brook charr (*Salvelinus fontinalis*), *Rhodococcus* sp. originally isolated from skin mucus of brook charr and added to the tank water twice a day at a concentration of 10^5 mL^{-1}, Boutin et al. (2013) observed that the bacteria did not colonize the skin mucus, but was detected in the biofilm of the tank. An interesting beneficial effect was noticed, the population of the pathogen *F. psychrophilum* decreased in water by modulating the water microbiota. Furthermore, the bacterial communities in water samples were more diverse than the skin mucus microbiota.

An interesting aspect of *Rhodococcus* was recently evaluated by Garai et al. (2021), as they investigated degradation of mycotoxin. This is highly relevant as mycotoxins are secondary metabolites of fungi, which are common in food, and from time to time also present in aquafeed (Pietsch, 2020).

MULTI-STRAIN PROBIOTICS

In aquaculture, multi-strain probiotics have been considered to be more effective than a single strain in aquaculture, and readers with special interest in this topic, are referred to the recent reviews of Melo-Bolivar et al. (2021).

CONCLUSIONS AND FURTHER DIRECTIONS

Nearly 90% of the global aquaculture production is carried out in countries in Asia, and the development is so fast that infectious disease outbreak happens regularly, and to solve this problem antibiotics are used with few regulations. However, the abuse of antibiotic treatment in aquaculture with tetracycline, β-lactams, sulfonamides, quinolones etc. results in development of antibiotic resistance in the pathogens, accumulation of residual in finfish products, depression of immune system, and translation of resistant genes to terrestrial animals and humans. Therefore action for alternative treatment methods in aquaculture are needed. In addition to the concept of probiotics, paraprobiotic is relatively established in higher vertebrate models and related food production sectors, but its application in aquaculture is still in its early stage (Choudhury and Kamilya, 2019; Teame et al., 2020), and merits investigations. Another alternative method is postbiotic that may be useful in aquaculture (Ang et al., 2020; Cuevas-González et al., 2020; Teame et al., 2020), a topic that merits further studies.

Moreover, peptides and exopolysaccharides revealed antimicrobial properties against bacterial pathogens, and SCFAs display both antimicrobial activities against bacterial pathogens and immune stimulating effects to aquatic organism, and cell surface proteins and teichoic acid can act as vaccine. Furthermore, it is well known that dietary manipulation affect the gut microbiota and improve fish health (e.g., Ringø et al., 2016; Turchini et al., 2022).

Dose as defined as the concentration (number of probiotic cells) must be carefully determined, as overdosing may result in lower efficacy with increasing costs, and under dosing could reduce the efficacy of the probiont. Previously, administration doses between 10^4 and 10^6 cells mL^{-1} to the total culture volume was suggested to be sufficient in introducing a probiotic capable of dominating the intestinal microbiota (Vine et al., 2006), but nowadays doses between 10^7 and 10^9 cells mL^{-1} are used. However, in order to maintain the desired probiotic concentration in the culture water,

additional doses may be required, and its frequency may depend on the probiotic species, stage of fish development, diet, culture conditions (Verschuere et al., 2000).

Even though focus has been directed towards LAB and bacilli within probiotics in aquaculture (e.g., Ringø et al., 2018; Ringø et al., 2020a; James et al., 2021; Nayak, 2021), we strongly recommend the scientific community to focus on other interesting probionts. They play important roles in mediating and stimulating GI development, aiding digestive function, maintaining mucosal tolerance, enhance the immune response, and provide protection against diseases, development of metabolic syndrome, vitamin synthesis, modulation of the gut microbiota, and interactions on the gut-brain axis and gut-kidney axis. In addition, multistrain probiotic administration increased the gut microbiota diversity (Halkjær et al., 2020) illustrating that the gut microbiota merits further investigation in finfish aquaculture.

Probiotic applications may be extended in aquaculture with the use of exo-enzymes producing strains in 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. Along with probiotic potential, studies should be directed to develop the probiotic-products as synbiotics or postbiotics and their efficacy in culture condition are required to be evaluated.

The beneficial effects of LAB and *Bacillus* and their bacteriocins as alternatives to antibiotic growth promoters in animal production is well known (e.g., Caulier et al., 2019; Vieco-Saiz et al., 2019). However, as no information is available on bacteriocins from other promising probiotics in aquaculture, we highly recommend that this topic receive more attention.

Bacteria communicate with one another using chemical signal molecules, a process, and termed quorum sensing (QS), the enzymatic degradation of AHLs, has been suggested as a promising strategy to control bacterial diseases (e.g., Defoirdt, 2018; Ghanei-Motlagh et al., 2020). For example, Ghanei-Motlagh et al. (2020) revealed that *Shewanella* isolated from Asian sea bass showed high ability to degrade synthetic- and natural AHLs produced by *V. harveyi* and *V. alginolyticus*.

Within the probiotic bacteria discussed in the present study, a topic that merits investigation is the interactions between probiotics and antioxidant properties, a topic reviewed by Wang et al. (2017).

Even though probiotic inclusion in the diet is the most frequently used administration method, several studies have administrated probiotics in the water (Jahangiri and Esteban, 2018; the present study). However, to fully conclude that water administration is a suitable method, further studies need to be conducted in intensive production.

In the conclusion, application of beneficial microbes is a sustainable approach.

AUTHOR CONTRIBUTIONS

ER: Introduction, *Acinetobacter*, *Alcaligenes*, *Aliivibrio*, *Arthrobacter*, *Bifidobacterium*, *Brochothrix*, *Chromobacterium*, *Clostridium*, *Enterovibrio*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Rhodococcus*, *Rhodopseudomonas*, *Shewanella* and editorial. XL: *Pseudomonas*, *Roseobacter*, *Vibrio* and *Rhodosporidium*. HD: *Aeromonas*, and *Alteromonas*. KG: proofreading, editing and provided critical feedback in revision. All authors contributed to the article and approved the submitted version.

FUNDING

The publication charges for this article have been funded by a grant from the publication fund of UiT The Arctic University of Norway.

REFERENCES

Abbass, A., Sharifuzzaman, S. M., and Austin, B. (2010). Cellular Components of Probiotics Control *Yersinia Ruckeri* Infection in Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum). *J. Fish Dis.* 33, 31–37. doi: 10.1111/j.1365-2761.2009.0186.x

Abdelhamed, H., Ozdemir, O., Waldbieser, G., Perkins, A. D., Lawrence, M. L., and Karsi, A. (2019). Effects of Florfenicol Feeding on Diversity and Composition of the Intestinal Microbiota of Channel Catfish (*Ictalurus* Punctatus. *Aquacult. Res.* 50, 3663–3672. doi: 10.1111/are.14325

Abd El-Rhman, A. M., Khattab, Y. A. E., and Shalaby, A. M. E. (2009). *Micrococcus Luteus* and *Pseudomonas* Species as Probiotics for Promoting the Growth Performance and Health of Nile Tilapia, *Oreochromis Niloticus*. *Fish Shellfish Immunol.* 27, 175–180. doi: 10.1016/j.fsi.2009.03.020

Aerts, J., Schaeck, M., De Swaef, E., Ampe, B., and Decostere, A. (2018). *Vibrio Lentus* as a Probiotic Candidate Lowers Glucocorticoid Levels in Gnotobiotic Sea Bass Larvae. *Aquaculture* 492, 40–45. doi: 10.1016/j.aquaculture.2018.03.059

Akayli, T., Albayrak, G., Urku, C., Canak, O., and Yoruk, E. (2016). Characterization of Micrococcus Luteus and Bacillus Marisflavi Recovered From Common Dentex (Dentex Dentex) Larviculture System. *Med. Mar. Sci.* 17 (1), 163–169. doi: 10.12681/mms.1322

Akayli, T., and Urku, C. (2014). A Study on Probiotic Bacteria Isolated From Common Dentex (*Dentex Dentex*) Larvae and Their Antagonistic Effect on *Photobacterium Damselae* Subsp Damselae. *Israeli J. Aquacult. Bamidgeh* 66, 100. doi: 10.46989/001c.20783

Akimoto, M., Ishii, T., Yamagaki, K., Ohtaguchi, K., Koide, K., and Yazawa, K. (1990). Production of Eicosapentaenoic Acid by a Bacterium Isolated From Mackerel Intestines. *J. Am. Oil Chem. Soc* 67 (12), 911–915. doi: 10.1007/BF02541846

Ang, C. Y., Sano, M., Dan, S., Leelakriangsak, M., and Lal, T. (2020). Postbiotics Applications as Infectious Disease Control Agent in Aquaculture. *Biocontrol Sci.* 25 (1), 1–7. doi: 10.4265/bio.25.1

Asaduzzaman, M., Ie.hata, S., Akter, S., Kader, M. A., Ghosh, S. K., Khan, M. N. A., et al. (2018). Effects of Host Gut-Derived Probiotic Bacteria on Gut Morphology, Microbiota Composition and Volatile Short Chain Fatty Acids Production of Malaysian Mahseer Tor Tambroides. *Aquacult. Rep.* 9, 53–61. doi: 10.1016/j.aqrep.2017.12.003

Austin, B., Stuckey, L., Robertson, P., Effendi, I., and Griffith, D. (1995). A Probiotic Strain of *Vibrio Alginolyticus* Effective in Reducing Diseases Caused by *Aeromonas Salmonicida*, *Vibrio Anguillarum* and *Vibrio Ordalii*. *J. Fish Dis.* 18, 93–96. doi: 10.1111/j.1365-2761.1995.tb01271.x

Bakke-McKellep, A. M., Penn, M. H., Salas, P. M., Refstie, S., Sperstad, S., Landsverk, T., et al. (2007). Effects of Dietary Soybean Meal, Inulin and

Oxytetracycline on Gastrointestinal Histological Characteristics, Distal Intestine Cell Proliferation and Intestinal Microbiota in Atlantic Salmon (*Salmo Salar* L.). *Brit. J. Nutr.* 97, 699–713. doi: 10.1017/S0007114507381397

Benediktsdottir, E., Verdonck, L., Sproer, C., Helgason, S., and Swings, J. (2000). Characterization of *Vibrio Viscosus* and *Vibrio Wodanis* Isolated at Different Geographical Locations: A Proposal for Reclassification of *Vibrio Viscosus* as *Moritella Viscosa* Comb. Nov. *Inter. J. Sys. Evol. Microbiol.* 50, 479–488. doi: 10.1099/00207713-50-2-479

Bermudez-Brito, M., Plaza-Diaz, J., Munoz-Quezada, S., Gomez-Llorente, C., and Gil, A. (2012). Probiotic Mechanisms of Action. *Ann. Nutr. Metab.* 61, 160–174. doi: 10.1159/000342079

Boutin, S., Audet, C., and Derome, N. (2013). Probiotic Treatment by Indigenous Bacteria Decreases Mortality Without Disturbing the Natural Microbiota of *Salvelinus Fontinalis*. *Can. J. Microbiol.* 59 (10), 662–670. doi: 10.1139/cjm-2013-0443

Brunt, J., and Austin, B. (2005). Use of a Probiotic to Control Lactococcosis and Streptococcosis in Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum). *J. Fish Dis.* 28 (12), 693–701. doi: 10.1111/j.1365-2761.2005.00672.x

Brunt, J., Hansen, R., Jamieson, D. J., and Austin, B. (2008). Proteomic Analysis of Rainbow Trout (*Oncorhynchus Mykiss*, Walbaum) Serum After Administration of Probiotics in Diets. *Vet. Immunol. Immunophathol.* 121 (3-4), 199–205. doi: 10.1016/j.vetimm.2007.09.010

Brunt, J., Newaj-Fyzul, A., and Austin, B. (2007). The Development of Probiotics for the Control of Multiple Bacterial Diseases of Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum). *J. Fish Dis.* 30 (10), 573–579. doi: 10.1111/j.1365-2761.2007.00836.x

Buchan, A., and Moran, M. A. (2005). Overview of the Marine *Roseobacter* Lineage. *Appl. Environ. Microbiol.* 71, 5665–5677. doi: 10.1128/AEM.71.10.5665-5677.2005

Bunnoy, A., Na-Nakorn, U., Kayansamruaj, P., and Srisapoome, P. (2019b). *Acinetobacter* Strain KU011TH, a Unique Organism Related to *Acinetobacter Pittii* and Isolated From the Skin Mucus of Healthy Bighead Catfish and its Efficacy Against Several Fish Pathogens. *Microorganisms* 7, 549. doi: 10.3390/microorganisms7110549

Bunnoy, A., Na-Nakorn, U., and Srisapoome, P. (2019a). Probiotic Effects of a Novel Strain, *Acinetobacter* KU011TH, on the Growth Performance, Immune Responses, and Resistance Against *Aeromonas Hydrophila* of Bighead Catfish (*Clarias Macrocephalus* Günther 1864). *Microorganisms* 7, 613. doi: 10.3390/microorganisms7120613

Burbank, D. R., Shah, D. H., LaPatra, S. E., Fornshell, G., and Cain, K. D. (2011). Enhanced Resistance to Coldwater Disease Following Feeding of Probiotic Bacterial Strains to Rainbow Trout (*Oncorhynchus Mykiss*). *Aquaculture* 321, 185–190. doi: 10.1016/j.aquaculture.2011.09.004

Cabello, F. C. (2006). Heavy Use of Prophylactic Antibiotics in Aquaculture: A Growing Problem for Human and Animal Health and for the Environment. *Environ. Microbiol.* 8, 1137–1144. doi: 10.1111/j.1462-2920.2006.01054.x

Cabello, F. C., Godfrey, H. P., Ivanova, L., Shah, S. Q. A., Sørum, H., and Tomova, A. (2020). Freshwater Salmon Aquaculture in Chile and Transferable Antimicrobial Resistance. *Environ. Microbiol.* 22 (2), 559–563. doi: 10.1111/j.1462-2920.14891

Cámara-Ruiz, M., Balebona, M. C., Morinigo, M.Á., and Esteban, M.Á. (2020). Probiotic *Shewanella Putrefaciens* (SpPdp11) as Fish Health Modulator: A Review. *Microorganisms* 8, 1990. doi: 10.3390/microorganisms8121990

Capkin, E., and Altinok, I. (2009). Effects of Dietary Probiotic Supplementations on Prevention/Treatment of Yersiniosis Disease. *J. Appl. Microbiol.* 106, 1147–1153. doi: 10.1111/j.1365-2672.2008.04080.x

Caulier, S., Nannan, C., Gillis, A., Licciardi, F., Bragard, C., and Mahillon, J. (2019). Overview of the Antimicrobial Compounds Produced by Members of the *Bacillus Subtilis* Group. *Front. Microbiol.* 10. doi: 10.3389/fmicb.2019.00302

Cerezuela, R., Guardiola, F. A., Cuesta, A., and Esteban, M. A. (2016). Enrichment of Gilthead Seabream (*Sparus Aurata* L.) Diet With Palm Fruit Extracts and Probiotics: Effects on Skin Mucosal Immunity. *Fish Shellfish Immunol.* 49, 100–109. doi: 10.1016/j.fsi.2015.12.028

Chabrillón, M., Arijo, S., Díaz-Rosales, P., Balebona, M. C., and Morinigo, M. A. (2006). Interference of *Listonella Anguillarum* With Potential Probiotic Microorganisms Isolated From Farmed Gilthead Seabream (*Sparus Aurata*, L.). *Aquacult. Res.* 37, 78–86. doi: 10.1111/j.1365-2109.2005.01400.x

Chabrillón, M., Rico, R. M., Arijo, S., Diaz-Rosales, P., Balebona, M. C., and Morinigo, M. A. (2005b). Interactions of Microorganisms Isolated From Gilthead Seabream, *Sparus Aurata* L., on *Vibrio Harveyi*, a Pathogen of Farmed Senegalese Sole, *Solea Senegalensis* (Kaup). *J. Fish Dis.* 28, 531–537. doi: 10.1111/j.1365-2761.2005.00657.x

Chabrillón, M., Rico, S., Balebona, M. C., and Morinigo, M. A. (2005a). Adhesion to Sole, *Solea Senegalensis* Kaup, Mucus of Microorganisms Isolated From Farmed Fish, and Their Interaction With *Photobacterium Damselae* Subsp. *Piscicida*. *J. Fish Dis.* 28, 229–237. doi: 10.1111/j.1365-2761.2005.00623.x

Chauhan, A., and Singh, R. (2019). Probiotics in Aquaculture: A Promising Emerging Alternative Approach. *Symbiosis* 77, 99–113. doi: 10.1007/s13299-018-0580-1

Chen, Z., Ceballos-Francisco, D., Guardiola, F. A., and Esteban, M.Á. (2020b). Dietary Administration of the Probiotic *Shewanella Putrefaciens* to Axperimentally Wounded Gilthead Seabream (*Sparus Aurata* L.) Facilitates the Skin Wound Healing. *Sci. Rep.* 10, 11029. doi: 10.1038/s41598-020-68024-z

Chen, Z., Ceballos-Francisco, D., Guardiola, F. A., and Esteban, M.Á. (2020c). Influence of Skin Wounds on the Intestinal Inflammatory Response and Barrier Function. Protective Role of Dietary *Shewanella Putrefaciens* SpPdp11 Administration to Gilthead Seabream (*Sparus Aurata* L.). *Fish Shellfish Immunol.* 99, 414–423. doi: 10.1016/j.fsi.2020.02.022

Chen, S., Liu, C., and Hu, S. (2019b). Dietary Administration of Probiotic *Paenibacillus Ehimensis* NPUST1 With Bacteriocin-Like Activity Improves Growth Performance and Immunity Against *Aeromonas Hydrophila* and *Streptococcus Iniae* in Nile Tilapia (*Oreochromis Niloticus*). *Fish Shellfish Immunol.* 84, 695–703. doi: 10.1016/j.fsi.2028.10.059

Chen, Y., Sagada, G., Xu, B., Chao, W., Zou, F., Ng, W.-K., et al. (2019a). Partial Replacement of Fishmeal With *Clostridium Autoethanogenum* Single-Cell Protein in the Diet for Juvenile Black Sea Bream (*Acanthopagrus Schlegelli*). *Aquacult. Res* 51 (3), 1000–1011. doi: 10.1111/are.14446

Chen, J., Sun, R., Pan, C., Sun, Y., Mai, B., and Li, Q. X. (2020a). Antibiotics and Food Safety in Aquaculture. *J. Agricult. Food Chem.* 68, 11908–11919. doi: 10.1021/acs.jafc.0c03996

Chen, Y., Zhu, X., Yang, Y., Han, D., Jin, J., and Xie, S. (2014). Effect of Dietary Chitosan on Growth Performance, Haematology, Immune Response, Intestinal Morphology, Intestine Microbiota and Disease Resistance in Gibel Carp (*Carassius Auratus Gibelio*). *Aquacult. Nutr.* 20, 532–546. doi: 10.1111/anu.12106

Cheng, G., Hao, H., Xie, S., Wang, X., Dai, M., Huang, L., et al. (2014). Antibiotic Alternatives: The Substitution of Antibiotics in Animal Husbandry? *Front. Microbiol.* 5. doi: 10.3389/fmicb.2014.00217

Chi, C., Jiang, B., Yu, X.-B., Liu, T.-Q., Xia, L., and Wang, G.-X. (2014). Effects of Three Strains of Intestinal Autochthonous Bacteria and Their Extracellular Products on the Immune Response and Disease Resistance of Common Carp, *Cyprinus Carpio*. *Fish Shellfish Immunol.* 36 (1), 9–18. doi: 10.1016/j.fsi.2013.10.003

Choudhury, T. G., and Kamilya, D. (2019). Paraprobiotics: An Aquaculture Perspective. *Rev. Aquacult.* 11, 1258–1270. doi: 10.1111/raq.12290

Collins, M. D., Jones, D., and Kroppenstedt, R. M. (1983). Reclassification of Brevibacterium-Imperiale (Steinhaus) and Corynebacterium-Laevaniformans (Dias and Bhat) in a Redefined Genus Microbacterium (Orla-Jensen), As Microbacterium-Imperiale Comb Nov and Microbacterium-Laevaniformans Nom Rev - Comb Nov. *Syst. Appl. Microbiol.* 4 (1), 65–78.

Cordero, H., Guardiola, F. A., Tapia-Paniagua, S. T., Cuesta, A., Meseguer, J., Balebona, M. C., et al. (2015). Modulation of Immunity and Gut Microbiota After Dietary Administration of Alginate Encapsulated *Shewanella Putrefaciens* Pdp11 to Gilthead Seabream (*Sparus Aurata* L.). *Fish Shellfish Immunol.* 45 (2), 608–618. doi: 10.1016/j.fsi.2015.05.010

Cordero, H., Mauro, M., Cuesta, A., Cammarata, M., and Esteban, M. A. (2016b). *In Vitro* Cytokine Profile Revealed Differences From Dorsal and Ventral Skin Susceptibility to Pathogen-Probiotic Interaction in Gilthead Seabream. *Fish Shellfish Immunol.* 56, 188–191. doi: 10.1016/j.fsi.2016.07.018

Cordero, H., Morcillo, P., Cuesta, A., Brinchmann, M. F., and Esteban, M. A. (2016c). Differential Proteome Profile of Skin Mucus of Gilthead Seabream (*Sparus Aurata*) After Probiotic Intake and/or Overcrowding Stress. *J. Proteo.* 132, 41–50. doi: 10.1016/j.jprot.2015.11.017

Cordero, H., Morcillo, P., Meseguer, J., Cuesta, A., and Esteban, M. A. (2016a). Effects of *Shewanella Putrefaciens* on Innate Immunity and Cytokine

Expression Profile Upon High Stocking Density of Gilthead Seabream Specimens. *Fish Shellfish Immunol.* 51, 33–40. doi: 10.1016/j.fsi.2016.02.008

Cude, W. N., and Buchan, A. (2013). Acyl-Honnoserine Lactone-Based Quorum Sensing in the *Roseobacter* Clade: Complex Cell-to-Cell Communication Controls Multiple Physiologies. *Front. Microbiol.* 4. doi: 10.3389/fmicb.2013.00336

Cuevas-González, P. F., Licega, A. M., and Aguilar-Toalá, J. E. (2020). Postbiotics and Parabiotics: From Concepts to Application. *Food Res. Inter.* 136, 109502. doi: 10.1016/j.foodre.2020.109502

D'Alvise, P. W., Lillebø, S., Prol-Garcia, M. J., Wergeland, H. I., Nielsen, K. F., Bergh, Ø., et al. (2012). *Phaeobacter Gallaeciensis* Reduces *Vibrio Anguillarum* in Cultures of Microalgae and Rotifers, and Prevents Vibriosis in Cod Larvae. *PlosOne* 7 (8), e43996. doi: 10.1371/journalpone.0043996

D'Alvise, P. W., Lillebø, S., Wergeland, H. I., Gram, L., and Bergh, Ø. (2013). Protection of Codlarvae From Vibriosis by *Phaeobacter* Spp.: A Comparison of Strains and Introduction Times. *Aquaculture* 384-387, 82–85. doi: 10.1016/j.aquaculture.2012.12.013

Dawood, M. A. O., and Koshio, S. (2016). Recent Advances in the Role of Probiotics and Prebiotics in Carp Aquaculture: A Review. *Aquaculture* 454, 243–251. doi: 10.1016/j.aquaculture.2015.12.033

Defoirdt, T. (2018). Quorum-Sensing Systems as Targets for Antivirulence Therapy. *Trend. Microbiol.* 26, 4. doi: 10.1016/j.tim.2017.10.005

De, B. C., Meena, D. K., Behera, B. K., Das, P., Das Mohapatra, P. K., and Sharma, A. P. (2014). Probiotics in Fish and Shellfish Culture: Immunomodulatory and Ecophysiological Responses. *Fish Physiol. Biochem.* 40, 921–971. doi: 10.1007/s10695-013-9897-0

de Melo Pereira, G. V., de Oliveira Coelho, B., Magalhães Jùnior, A. I., Thomaz-Soccol, V., and Soccol, C. R. (2018). How to Select a Probiotic? A Review and Update of Methods and Criteria. *Biotechnol. Adv.* 36, 2060–2076. doi: 10.1016/j.biotechadv.2018.09.003

DeSchrijver, R., and Ollevier, F. (2000). Protein Digestion in Juvenile Turbot (*Scophthalmus Maximus*) and Effects of Dietary Administration of *Vibrio Proteolyticus*. *Aquaculture* 186, 107–116. doi: 10.1016/S0044-8486(99)00372-5

Díaz-Rosales, P., Arijo, S., Chabrillón, M., Alarcon, F. J., Tapia-Paniagua, S. T., Martinez-Manzanares, E., et al. (2009). Effects of Two Closely Related Probiotics on Respiratory Burst Activity of Senegalese Sole (*Solea Senegalensis*, Kaup) Phagocytes, and Protection Against Photobacterium Damselae Subsp. *Piscicida*. *Aquaculture* 293, 16–21. doi: 10.1016/j.aquaculture.2009.03.050

Diaz-Rosales, P., Salinas, I., Rodríguez, A., Cuesta, A., Chabrillón, M., Balebona, M. C., et al. (2006). Gilthead Seabream (*Sparus Aurata* L.) Innate Immune Response After Dietary Administration of Heat-Inactivated Potential Probiotics. *Fish Shellfish Immunol.* 20, 482–492. doi: 10.1016/j.fsi.2005.06.007

Dimitroglou, A., Merrifield, D. L., Carnevali, O., Picchietti, S., Avella, M., Daniels, C., et al. (2011). Microbial Manipulations to Improve Fish Health and Production - A Mediterranean Perspective. *Fish Shellfish Immunol.* 30 (1), 1–16. doi: 10.1016/j.fsi.2010.08.009

Dittmann, K. K., Rasmussen, B. B., Melchiorsen, J., Sonnenschein, E. C., Gram, L., and Bentzon-Tilia, M. (2020). Changes in the Microbiome of Mariculture Feed Organisms After Treatment With a Potentially Probiotic Strain of *Phaeobacter Inhibens*. *Appl. Environ. Microbiol.* 86 (14), e00499–e00420. doi: 10.1128/AEM.00499-20

Eddy, S. D., and Jones, S. H. (2002). Microbiology of Summer Flounder *Paralichthys Dentatus* Fingerling Production at a Marine Fish Hatchery. *Aquaculture* 211 (1-4), 9–28. doi: 10.1016/j.fsi.2005.06.007

Egerton, S., Culloty, S., Whooley, J., Stanton, C., and Ross, R. P. (2018). The Gut Microbiota of Marine Fish. *Front. Microbiol.* 9. doi: 10.3389/fmicb.2018.00873

Esteban, M. A., Cordero, H., Martinez-Tome, M., Jimenez-Monreal, A. M., Bakhrouf, A., and Mahdhi, A. (2014). Effect of Dietary Supplementation of Probiotics and Palm Fruits Extracts on the Antioxidant Enzyme Gene Expression in the Mucosae of Gilthead Seabream (*Sparus Aurata* L.). *Fish Shellfish Immunol.* 39 (2), 532–540. doi: 10.1016/j.fsi.2014.06.012

Feckaninova, A., Koscova, J., Mudronova, D., Popelka, P., and Toropilova, J. (2017). The Use of Probiotic Bacteria Against *Aeromonas* Infections in Salmonid Aquaculture. *Aquaculture* 469, 1–8. doi: 10.1016/j.aquaculture.2016.11.042

Fjellheim, A. J., Klinkenberg, G., Skjermo, J., Aasen, I. M., and Vadstein, O. (2010). Selection of Candidate Probionts by Two Different Strategies From Atlantic Cod (*Gadus Morhua* L.) Larvae. *Vet. Microbiol.* 144, 153–159. doi: 10.1016/j.vetmic.2009.12.032

Fjellheim, A. J., Playfoot, K. J., Skjermo, J., and Vadstein, V. (2007). Vibrionaceae Dominates the Microflora Antagonistic Towards *Listonella Anguillarum* in the Intestine of Cultured Atlantic Cod (*Gadus Morhua* L.) Larvae. *Aquaculture* 269 (1-4), 98–106. doi: 10.1016/j.aquaculture.2007.04.021

Fonseca, F., Cerqueira, R., and Fuentes, J. (2019). Impact of Ocean Acidification on the Intestinal Microbiota of the Marine Sea Bream (*Sparus Aurata* L.). *Front. Physiol.* 10. doi: 10.3389/fphys.2019.01446

Fuller, R. (1989). Probiotics in Man and Animals. *J. Appl. Bacteriol.* 66 (5), 365–378.

Fu, L., Zhang, X., Wang, Y., Peng, L., and Li, W. (2017). Nitrogen Removal Characteristics of *Pseudomonas Stutzeri* F11 and its Application in Grass Carp Culture. *Fish. Sci.* 83, 89–98. doi: 10.1007/s12562-016-1038-0

Gao, Q., Xiao, C., Min, M., Zhang, C., Peng, S., and Shi, Z. (2016). Effects of Probiotics Dietary Supplementation on Growth Performance, Innate Immunity and Digestive Enzymes of Silver Pomfret, *Pampus Argenteus*. *Indian J. Anim. Res.* 50 (6), 936–941. doi: 10.18805/ijar.9640

Gao, Q., Xiao, Y., Sun, P., Peng, S., Yin, F., Ma, X., et al. (2013). *In Vitro* Protective Efficacy of *Clostridium Butyricum* Against Fish Pathogen Infections. *Indian J. Microbiol.* 53 (4), 453–459. doi: 10.1007/s12088-013-0394-z

Garai, E., Risa, A., Varga, E., Cserháti, M., Kriszt, B., Urbányi, B., et al. (2021). Evaluation of the Multimycotoxin-Degrading Efficiency of *Rhodococcus Erythropolis* NI1 Strain With the Three-Step Zebrafish Microinjection Method. *Intern. J. Mol. Sci.* 22, 724. doi: 10.3390/ijms22020724

Garcia de la Banda, I., Lobo, C., León-Rubio, J. M., Tapia-Paniagua, S., Balebona, M. C., Morinigo, M. A., et al. (2010). Influence of Two Closely Related Probiotics on Juvenile Senegalese Sole (*Solea Senegalensis*, Kaup 1858) Performance and Protection Against *Photobacterium Damselae* Subsp. *Piscicida*. *Aquaculture* 306, 281–288. doi: 10.1016/j.aquaculture.2010.05.008

Garcia de la Banda, I., Lobo, C., Mariana, C., Leon-Rubio, J. M., Salvador, A., GemaPazos, L. M. L., et al. (2012). Influence of Dietary Administration of a Probiotic Strain *Shewanella Putrefaciens* on Senegalese Sole (*Solea Senegalensis*, Kaup 1858) Growth, Body Composition and Resistance to *Photobacterium Damselae* Subsp. *Piscicida*. *Aquacult. Res.* 43 (5), 662–669. doi: 10.1111/j.1365-2109.2011.02871.x

Gatesoupe, F. J. (1997). Siderophore Production and Probiotic Effect of Vibrio Sp. Associated With Turbot Larvae, *Scophthalmus Maximus*. *Aqua. Living Res.* 10, 239–246. doi: 10.1051/alr:1997026

Gatesoupe, F. J. (1999). The Use of Probiotics in Aquaculture. *Aquaculture* 180, 147–165. doi: 10.1016/S0044-8486(99)00187-8

Gauthier, G., Gauthier, M., and Christen, R. (1995). Phylogenetic Analysis of the Genera *Alteromonas*, *Shewanella*, and *Moritella* Using Genes Coding for Small-Subunit rRNA Sequences and Division of the Genus *Alteromonas* Into Two Genera, *Alteromonas* (Emended) and *Pseudoalteromonas* Gen. Nov., and Proposal of Twelve New Species Combinations. *Inter. J. Sys. Bacteriol.* 45 (4), 755–761. doi: 10.1099/00207713-45-4-755

Geng, X., Dong, X. H., Tan, B. P., Yang, Q. H., and Chi, S. Y. (2012a). Effects of Dietary Chitosan and *Bacillus Subtilis* on the Growth Performance, non-Specific Immunity and Disease Resistance of Cobia, (*Rachycentron Canadum*). *Fish Shellfish Immunol.* 31, 400–406. doi: 10.1016/j.fsi.2011.06.006

Ghanei-Motlagh, R., Mohammadian, T., Gharibi, D., Menanteau-Ledouble, S., Mahmoudi, E., Khosravi, M., et al. (2020). Quorum Quenchingpproperties and Probiotic Potentials of Intestinal Associated Bacteria in Asian Sea Bass *Lates Calcarifer*. *Mar. Drugs* 18, 23. doi: 10.3390/md18010023

Girijakumari, N. R., Ethiraja, K., and Marimuthu, P. ,. N. (2018). In Vitro and *In Vivo* Evaluation of Probiotic Properties of *Enterobacter Cloacae* in Kenyi Cichlid, *Maylandia Lombardoi*. *Aquacult. Inter.* 26, 959–980. doi: 10.1007/s10499-018-0262-2

Giri, S. S., Jun, J. W., Yun, S., Kim, H. J., Kim, S. G., Kim, S. W., et al. (2020). Effects of Dietary Heat-Killed *Pseudomonas Aeruginosa* Strain VSG2 on Immune Functions, Antioxidant Efficacy, and Disease Resistance in *Cyprinus Carpio*. *Aquaculture* 514, 734489. doi: 10.1016/j.aquaculture.2019.734489

Giri, S. S., Sen, S. S., Chi, C., Kim, H. J., Yun, S., and Park, S. C. (2015). Effects of Cellular Products of Potential Bacteria on the Immune Response of *Labeo Rohita* and Susceptibility to *Aeromonas Hydrophila* Infection. *Fish Shellfish Immunol.* 46, 716–722. doi: 10.1016/j.fsi.2015.08.012

Giri, S. S., Sen, S. S., Jun, J. W., Park, S. C., and Sukumara, V. (2016). Heat-Killed Whole-Cell Products of the Probiotic *Pseudomonas Aeruginosa* VSG2 Strain

Affect *In Vitro* Cytokine Expression in Head Kidney Macrophages of *Labeo Rohita*. *Fish Shellfish Immunol.* 50, 310–316. doi: 10.1016/j.fsi.2016.02.007

Giri, S. S., Sen, S. S., and Sukumaran, V. (2012). Effects of Dietary Supplementation of Potential Probiotic *Pseudomonas Aeruginosa* VSG-2 on the Innate Immunity and Disease Resistance of Tropical Freshwater Fish, *Labeo Rohita*. *Fish Shellfish Immunol.* 32, 1135–1140. doi: 10.1016/j.fsi.2012.03.019

Giri, S. S., Sukumaran, V., Sen, S. S., Vinumonia, J., Banu, B. N., and Jena, P. K. (2011). Antagonistic Activity of Cellular Components of Potential Probiotic Bacteria, Isolated From the Gut of *Labeo Rohita*, Against *Aeromonas Hydrophila*. *Prob. Antimicro. Prot.* 3 (3-4), 214–222. doi: 10.1007/s12602-011-9078-3

González-Palacios, C., Fregeneda-Grandes, J.-M., and Aller-Gancedo, J.-M. (2019). Biocontrol of Saprolegniosis in Rainbow Trout (*Oncorhynchus Mykiss* Walbaum) Using Two Bacterial Isolates (LE89 and LE141) of *Pseudomonas Fluorescens*. *J. Fish Dis.* 42, 269–275. doi: 10.1111/jfd.12928

González-Palacios, C., Fregeneda-Grandes, J.-M., and Aller-Gancedo, J.-M. (2020). Possible Mechanisms of Action of Two *Pseudomonas Fluorescens* Isolates as Probiotics on Saprolegniosis Control in Rainbow Trout (*Oncorhynchus Mykiss* Walbaum). *Animals* 10, 1507. doi: 10.3390/ani10091507

Gram, L., Lovold, T., Nielsen, J., Melchiorsen, J., and Spangaard, B. (2001). In Virto Antagonism of the Probiont *Pseudomonas Fluorecens* AH2 Against *Aeromonas Salmonicida* Does Not Confer Protection of Salmon Against Furunculosis. *Aquaculture* 199 (1-2), 1–11. doi: 10.1016/S0044-8486(01)00565-8

Gram, L., Melchiorsen, J., Spanggaard, B., Huber, I., and Nielsen, T. (1999). Inhibition of *Vibrio Anguillarum* by *Pseudomonas Fluorescens* Strain AH2 a Possible Probiotic Treatment of Fish. *Appl. Environ. Microbiol.* 65 (3), 969–973. doi: 10.1128/AEM.65.3.969-973.1999

Green, T. J., Smullen, R., and Barnes, A. C. (2013). Dietary Soybean Protein Concentrate-Induced Intestinal Disorder in Marine Farmed Atlantic Salmon, *Salmo Salar* is Associated With Alterations in Gut Microbiota. *Vet. Microbiol.* 166 (1-2), 286–292. doi: 10.1016/j.vetmic.2013.05.009

Gudmundsdottir, B. K., and Bjornsdottir, B. (2007). Vaccination Against Atypical Furunculosis and Winter Ulcer Disease of Fish. *Vaccine* 25 (30), 5512–5523. doi: 10.1016/j.vaccine.2007.02.009

Guo, P., Zhang, K., Ma, X., and He, P. (2020). *Clostridium* Species as Probiotics: Potential and Challenges. *J. Anim. Sci. Biotechnol.* 11, 24. doi: 10.1186/s40104-019-0402-1

Gupta, A., Gupta, P., and Dhawan, A. (2014). Dietary Supplementation of Probiotics Affects Growth, Immune Response and Disease Resistance of *Cyprinus Carpio* Fry. *Fish Shellfish Immunol.* 41 (2), 113–119. doi: 10.1016/j.fsi.2014.08.023

Gupta, A., Gupta, P., and Dhawan, A. (2016). *Paenibacillus Polymyxa* as a Water Additive Improved Immune Response of *Cyprinus Carpio* and Disease Resistance Against *Aeromonas Hydrophila*. *Aquacult. Rep.* 4, 86–92. doi: 10.1016/j.aqrep.2016.07.002

Guzmán-Villanueva, L. T., Tovar-Ramírez, D., Gisbert, E., Cordero, H., Guardiola, F. ,. A., Cuesta, A., et al. (2014). Dietary Administration of β-1,3/1,6-Glucan and Probiotic Strain Shewanella Putrefaciens, Single or Combined, on Gilthead Seabream Growth, Immune Responses and Gene Expression. *Fish Shellfish Immunol.* 39, 34–41. doi: 10.1016/j.fsi.2014.04.024

Halkjær, S. I., de Knegt, V. E., Lo, B., Nilas, L., Cortes, D., Pedersen, A. E., et al. (2020). Multistrain Probiotic Increases the Gut Microbiota Diversity in Obese Pregnant Women: Results From a Randomized, Double-Blind Placebo-Controlled Study. *Curr. Dev. Nutr.* 4 (7), nzaa095. doi: 10.1093/cdn/nzaa095

Hamilton, E. F., Element, G., van Coeverden de Groot, P., Engel, K., Neufeld, J. D., Shah, V., et al. (2019). Anadromous Arctic Char Microbiomes: Bioprospecting in the High Arctic. *Front. Bioeng. Biotechnol.* 7. doi: 10.3389/fbioe.2019.00032

Hao, K., Wu, Z. Q., Li, D. L., Yu, X. B., Wang, G. X., and Ling, F. (2017). Effects of Dietary Administration of *Shewanella Xiamenensis* A-1, *Aeromonas Veronii* A-7, and *Bacillus Subtilis*, Single or Combined, on the Grass Carp (*Ctenopharyngodon Idella*) Intestinal Microbiota. *Prob. Antimicro. Prot.* 9 (4), 386–396. doi: 10.1007/s12602-017-9269-7

Hassani, M. H. S., Jourdehi, A. Y., Zelti, A. H., Masouleh, A. S., and Lakani, F. B. (2020). Effects of Commercial Superzist Probiotic on Growth Performance and Hematological and Immune Indices in Fingerlings *Acipenser Baerii*. *Aquacult. Inter.* 28 (1), 377–387. doi: 10.1007/s10499-019-00468-1

Hayatgheib, N., Moreau, E., Calvez, S., Lepelletier, D., and Pouliquen, H. (2020). A Review of Functional Feeds and the Control of *Aeromonas* Infections in Freshwater Fish. *Aquacult. Inter.* 28 (3), 1083–1123. doi: 10.1007/s10499-020-00514-3

He, R.-P., Feng, J., Tian, X.-L., Dong, S.-L., and Wen, B. (2017). Effects of Dietary Supplementation of Probiotics on the Growth, Activities of Digestive and non-Specific Immune Enzymes in Hybrid Grouper (*Epinephelus Lanceolatus* ♂ X *Epinephelus Fuscoguttatus* ♀). *Aquacult. Res.* 48, 5782–5790. doi: 10.1111/are.13401

Higuera-Llanten, S., Vasquez-Ponce, F., Barrientos-Espinoza, B., Mardones, F., Marshall, S., and Olivares-Pacheco, J. (2018). Extended Antibiotic Treatment in Salmon Farms Select Multiresistant Gut Bacteria With a High Prevalence of Antibiotic Resistance Genes. *PLoSOne* 13 (9), e0203641. doi: 10.1371/journal.pone.0202641

Hjelm, M., Bergh, Ø., Riaza, A., Nielsen, J., Melchiorsen, J., Jensen, S., et al. (2004). Selection and Identification of Autochtonous Potential Probiotic Bacteria From Turbot Larvae (*Scophthalmus Maximus*) Rearing Units. *Sys. Appl. Microbiol.* 27, 360–371. doi: 10.1078/0723-2020-00256

Hoque, F., Jawahar, Abraham, T., Nagesh, T. S., and Kamilya, D. (2019). *Pseudomonas Aeruginosa* FARP72 Offers Protection Against *Aeromonas Hydrophila* Infection in *Labeo Rohita*. *Probio. Anti Prot.* 11 (3), 973–980. doi: 10.1007/s12602-018-9456-1

Hoseinifar, S. H., Sun, Y.-Z., Wang, A., and Zhou, Z. (2018). Probiotic as Means of Diseases Control in Aquaculture, a Review of Current Knowledge and Future Perspectives. *Front. Microbiol.* 9. doi: 10.3389/fmicb.2018.02429

Hoseinifar, S. H., Yousefi, S., van Doan, H., Ashouri, G., Gioacchini, G., Maradonna, F., et al. (2020). Oxidative stress and antioxidant defense in fish: The implications of probiotic, prebiotic, and synbiotics. *Rev. Fish. Sci. Aquacult* 29 (2), 198–217. doi: 10.1080/23308249.2020.1795616

Hu, H., Mai, K. S., Zhang, Y. J., Ai, Q. H., Xu, W., Zhang, W. B., et al. (2015). Effects of Dietary Xylan on Growth Performance, Digestive Enzyme Activity and Intestinal Morphology of Juvenile Turbot (*Scophthalmus Maximus* L.). *Israeli J. Aquacult. Bamidgeh* 67, 115. doi: 10.46989/001c.20730

Hu, J., Yao, Y., Yang, Y., Gao, C., Zhang, F., Xia, R., et al. (2021). Advances in Intra-Species Molecular Typing Analysis of Aquatic Probiotics Approved by the Chinese Ministry of Agriculture. *Rev. Aquacult* 13 (1), 178–188. doi: 10.1111/raq.12469

Ina-Salwany, M. Y., Al-saari, N., Mohamad, A., Mursidi, F. A., Mohd-Aris, A., Amal, M. N. A., et al. (2019). Vibriosis in Fish: A Review on Disease Development and Prevention. *J. Aqua. Anim. Health* 31 (1), 2–22. doi: 10.1002/aah.10045

Irianto, A., and Austin, B. (2002a). Probiotics in Aquaculture. *J. Fish Dis.* 25 (11), 633–642. doi: 10.1046/j.1365-2761.2002.00422.x

Irianto, A., and Austin, B. (2002b). Use of Probiotics to Control Furunculosis in Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum). *J. Fish Dis.* 25 (6), 333–342. doi: 10.1046/j.1365-2761.2002.00375.x

Irianto, A., and Austin, B. (2003a). Use of Dead Probiotic Cells to Control Furunculosis in Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum). *J. Fish Dis.* 26, 59–62. doi: 10.1046/j.1365-2761.2003.00414.x

Irianto, A., and Austin, B. (2003b). Oral Administration of Formalin-Inactivated Cells of *Aeromonas Hydrophila* A3-51 Controls Infection by Atypical *A. Salmonicida* in Goldfish, *Carassius Auratus* (L.). *J. Fish Dis.* 26, 117–120. doi: 10.1046/j.1365-2761.2003.00439.x

Jahangiri, L., and Esteban, M. A. (2018). Administration of Probiotics in the Water in Finfish Aquaculture Systems: A Review. *Fishes* 3, 33. doi: 10.3390/fishes3030033

James, G., Das, B. C., Jose, S., and Kuma, R. V. J. (2021). *Bacillus* as an Aquaculture Friendly Microbe. *Aquacult. Intern.* 29, 323–353. doi: 10.1007/s10499-020-00630-0

Jan, A. T. (2017). Outer Membrane Vesicles (OMVs) of Gram-Negative Bacteria: A Perspective Update. *Front. Microbiol.* 8. doi: 10.3389/fmicb.2017.01043

Jiang, Y., Zhang, Z., Wang, Y. G., Jing, Y. Y., Liao, M. J., Rong, X. J., et al. (2018). Effects of Probiotic on Microfloral Structure of Live Feed Used in Larval Breeding of Turbot *Scophthalmus Maximus*. *J. Ocenol. Limnol.* 36 (3), 1002–1012. doi: 10.1007/s00343-018-7049-1

Jin, G. A., Wang, S. S., Yu, M., Yan, S. L., and Zhang, X. H. (2010). Identification of a Marine Antagonistic Strain JG1 and Establishment of a Polymerase Chain Reaction Detection Technique Based on the gyrB Gene. *Aquacult. Res.* 41 (12), 1867–1874. doi: 10.1111/j.1365-2109.2010.02591.x

Jurado, J., Villasanta-Gonzalez, A., Tapia-Paniagua, S. T., Balebona, M. C., de la Banda, I. G., Morinigo, M. A., et al. (2018). Dietary Administration of the Probiotic *Shewanella Putrefaciens* Pdp11 Promotes Transcriptional Changes of Genes Involved in Growth and Immunity in *Solea Senegalensis* Larvae. *Fish Shellfish Immunol.* 77, 350–363. doi: 10.1016/j.fsi.2018.04.018

Karlsen, C., Ottem, K. F., Brevik, O. J., Davey, M., Sørum, H., and Winther-Larsen, H. C. (2017). The Environmental and Host-Associated Bacterial Microbiota of Arctic Sea-Water-Farmed Atlantic Salmon With Ulcerative Disorders. *J. Fish Dis.* 40 (11), 1645–1663. doi: 10.1111/jfd.12632

Kesarcodi-Watson, A., Kaspar, H., Lategan, M. J., and Gibson, L. (2012). Performance of Single and Multi-Strain Probiotics During Hatchery Production of Greenshell (TM) Mussel Larvae, *Perna Canaliculus*. *Aquaculture* 354, 56–53. doi: 10.1016/j.aquaculture.2012.04.026

Kim, A., Kim, N., Roh, H. J., Chun, W.-K., Ho, D. T., Lee, Y., et al. (2019). Administration of Antibiotics can Cause Dysbiosis in Fish Gut. *Aquaculture* 512, 734330. doi: 10.1016/j.aquaculture.2019.734330

Kim, J. K., Lee, B. K., Kim, S. H., and Moon, J. H. (1999). Characterization of Denitrifying Photosynthetic Bacteria Isolated From Photosynthetic Sludge. *Aquacult. Eng.* 19 (3), 179–193. doi: 10.1016/S0144-8609(98)00050-8

Klakegg, Ø., Salonius, K., Nilsen, A., Fülberth, M., and Sørum, H. (2020a). Enhanched Growth and Decreased Mortality in Atlantic Salmon (*Salmo Salar*) After Probiotic Bath. *J. Appl. Microbiol.* 129, 146–160. doi: 10.1111/jam.14649

Klakegg, Ø., Salonius, K., Nilsen, A., Fülberth, M., and Sørum, H. (2020b). Improved Health and Better Survival of Farmed Lumpfish (*Cyclopterus Lumpus*) After a Probiotic Bath With Two Strains of *Aliivibrio*. *Aquaculture* 518, 734810. doi: 10.1016/aquaculture.2019.734810

Korkea-aho, T. L., Papadoupoulou, A., Heikkinen, J., von Wright, A., Adams, A., Austin, B., et al. (2012). *Pseudomonas* Sp. M162 Confers Protection Against Rainbow Trout Fry Syndrome by Stimulating Immunity. *J. Appl. Microbiol.* 113, 24–35. doi: 10.1111/j.1365-2672.2012.05325.x

Kozasa, M. (1986). Toyocerin *_Bacillus Toyoi* as Growth Promotor for Animal Feeding. *Microbiol. Aliment. Nutr.* 4, 121–135.

Kuebutornye, F. K. A., Abarike, E. D., and Lu, Y. (2019). A Review on the Application of *Bacillus* as Probiotics in Aquaculture. *Fish Shellfish Immunol.* 87, 820–828. doi: 10.1016/j.fsi.2019.02.010

Kumar, V., Roy, S., Kumar Meena, D., and Kumar Sarkar, U. (2016). Application of Probiotics in Shrimp Aquaculture: Importance, Mechanisms of Action, and Methods of Administration. *Rev. Fish. Sci. Aquacult.* 24 (4), 342–358. doi: 10.1080/23308249.2016.119341

Labella, A. M., Arahal, D. R., Castro, D., Lemos, M. L., and Borrego, J. J. (2017). Revisiting the Genus *Photobacterium*: Taxonomy, Ecology and Pathogenesis. *Int. Microbiol.* 20 (1), 1–10. doi: 10.2436/20.1501.280

Lategan, M. J., Torpy, F. R., and Gibson, L. F. (2004). Biocontrol of Saprolegniosis in Silver Perch *Bidyanus Bidyanus* (Mitchell) by *Aeromonas Media* Strain A199. *Aquaculture* 235, 77–88. doi: 10.1016/j.aquaculture.2003.09.014

Lauzon, H. L., Gudmundsdottir, S., Steinarsson, A., Oddgeirsson, M., Petursdottir, S. K., Reynisson, E., et al. (2010). Effects of Bacterial Treatment at Early Stages of Atlantic Cod (*Gadus Morhua* L.) on Larval Survival and Development. *J. Appl. Microbiol.* 108, 624–632. doi: 10.1111/j.1365-2672.2009.04454.x

Lazado, C. C., Caipang, C. M. A., and Estante, E. G. (2015). Prospects of Host-Associated Microorganisms in Fish and Penaeids as Probiotics With Immunomodulatory Functions. *Fish Shellfish Immunol.* 45, 2–12. doi: 10.1016/j.fsi.2015.02.023

Legrand, T. P. R. A., Catalano, S. R., Wos-Oxley, M. L., Wynne, J. W., Weyrich, L. S., and Oxley, A. P. A. (2020). Antibiotic-Induced Alterations and Repopulation Dynamics of Yellowtail Microbiota. *Anim. Microb.* 2, 26. doi: 10.1186/s42523-020-00046-4

Li, Z., Bao, N., Ren, T., Han, Y., Jiang, Z., Bai, Z., et al. (2019a). The Effect of Multi-Strain Probiotic on Growth Performance, non-Specific Immune Response, and Intestinal Health of Juvenile Turbot, *Scophthalmus Maximus* L. *Fish Physiol. Biochem.* 15, 1393–1407. doi: 10.1007/s10695-019-00635-4

Li, T., Ke, F., Gui, J.-F., Zhou, L., Zhang, X.-J., and Zhang, Q.-Y. (2019d). Protective Effect of *Clostridium Butyricum* Against *Carassius Auratus* Herpesvirus in Gibel Carp. *Aquacult. Inter.* 27 (3), 905–914. doi: 10.1007/s10499-019-00377-3

Linh, N. T. H., Nagai, S., Nagasaka, N., Okane, S., and Taoka, Y. (2018). Effect of *Lactococcus Lactis* K-C2 on the Growth Performance, Amino Acid Content and Gut Microflora of Amberjack *Seriola Dumerili*. *Fish. Sci.* 84 (6), 1051–1062. doi: 10.1007/s12562-018-1243-0

Liu, Y., Chen, Z., Dai, J., Yang, P., Xu, W., Ai, Q., et al. (2019). Sodium Butyrate Supplementation in High-Soybean Meal Diets for Turbot (*Scophthalmus Maximus*): Effects on Inflammatory Status, Mucosal Barriers and Microbiota in the Intestine. *Fish Shellfish Immunol.* 88, 65–75. doi: 10.1016/j.fsi.2019.02.064

Liu, R. J., Wu, W. S., Xu, X. H., Wang, Y. L., Yu, T., Wang, J. H., et al. (2020). *Rhodopseudomonas Palustris* in Effluent Enhances the Disease Resistance, TOR and NF-Kappa B Signalling Pathway, Intestinal Microbiota and Aquaculture Water Quality of *Pelteobagrus Vachelli*. *Aquacult. Res.* 51 (10), 3959–3971. doi: 10.1111/are.14736

Liu, Z. G., Zheng, A. F., Chen, M. M., Lian, Y. X., Zhang, X. K., Zhang, S. Z., et al. (2018). Isolation and Identification of Pathogenic *Aeromonas Veronii* From a Dead Yangtze Finless Porpoise. *Dis. Aquat. Org.* 132 (1), 13–22. doi: 10.3354/dao03288

Li, C., Zhang, B., Wang, X., Pi, X., Wang, X., Zhou, H., et al. (2019b). Improved Utilization of Soybean Meal Through Fermentation With Commensal Shewanella Sp. MR-7 in Turbot (Scophthalmus Maximus L.). *Micro. Cell Fact* 18, 214. doi: 10.1186/s12934-019-1265-z

Li, H., Zhou, Y., Ling, H., Luo, L., Qi, D., and Feng, L. (2019c). The Effect of Dietary Supplementation With *Clostridium Butyricum* on the Growth Performance, Immunity, Intestinal Microbiota and Disease Resistance of Tilapia (*Oreochromis Niloticus*). *PLoSOne* 14 (12), e0223428. doi: 10.1371/journal.pone.0223428

Lobo, C., Martin, M. V., Moreno-Ventas, X., Tapia-Paniagua, S. T., Rodriguez, C., Morinigo, M. A., et al. (2016). *Shewanella Putrefaciens* PdP11 Probiotic Supplementation as Enhancer of *Artemia* N-3 HUFA Contents and Growth Performance in Senegalese Sole Larviculture. *Aquacult. Nutr.* 24 (1), 548–561. doi: 10.1111/anu.12587

Lobo, C., Moreno-Ventas, X., Tapia-Paniagua, S., Rodriguez, C., Morinigo, M. A., and de la Banda, I. G. (2014a). Dietary Probiotic Supplementation (*Shewanella Putrefaciens* Pdp11) Modulates Gut Microbiota and Promotes Growth and Condition in Senegalese Sole Larviculture. *Fish Physiol. Biochem.* 40 (1), 295–309. doi: 10.1007/s10695-013-9844-0

Lobo, C., Tapia-Paniagua, S., Moreno-Ventas, X., Alarcon, F. J., Rodriguez, C., Balebona, M. ,. C., et al. (2014b). Benefit of Probiotic Administration on Growth and Performance Along Metamorphosis and Weaning of Senegalese Sole (*Solea Senegalensis*). *Aquaculture* 40 (1), 295–309. doi: 10.1016/j.aquaculture.2014.06.011

Lulijwa, R., Rupia, E. J., and Alfaro, A. C. (2020). Antibiotic Use in Aquaculture, Policies and Regulation, Health and Environmental Risks: A Review of the Top 15 Major Producers. *Rev. Aquacult.* 12, 640–663. doi: 10.1111/raq.12344

Lu, Q., Xi, L., Liu, Y., Gong, Y., Su, J., Han, D., et al. (2021). Effects of Dietary Inclusion of *Clostridium Autoethanogenum* Protein on the Growth Performance and Liver Health of Largemouth Bass (*Micropterus Salmoides*). *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.764964

Makled, S. O., Hamdan, A. M., and El-Sayed, A. F. M. (2020). Growth Promotion and Immune Stimulation in Nile Tilapia, *Oreochromis Niloticus*, Fingerlings Following Dietary Administration of a Novel Marine Probiotic, *Psychrobacter Maritimus* S. *Prob. Antimicrob. Prot.* 12 (2), 365–374. doi: 10.1007/s12602-019-09575-0

Makled, S. O., Hamdan, A. M., El-Sayed, A. F. M., and Hafez, E. E. (2017). Evaluation of Marine Psychrophile, *Psychrobacter Namhaensis* SO89, as a Probiotic in Nile Tilapia (*Oreochromis Niloticus*) Diets. *Fish Shellfish Immunol.* 61, 194–200. doi: 10.1016/j.fsi.2017.01.001

Makridis, P., Bergh, Ø., Skjermo, J., and Vadstein, O. (2001). Addition of Bacteria Bioencapsulated in *Artemia Metanauplii* to a Rearing System for Halibut Larvae. *Aquacult. Inter.* 9, 225–235. doi: 10.1023/A:1016815929846

Makridis, P., Martins, S., Reis, J., and Dinis, M. T. (2008). Use of Probiotic Bacteria in the Rearing of Senegalese Sole (*Solea Senegalensis*) Larvae. *Aquacult. Res.* 39, 627–634. doi: 10.1111/j.1365-2109.2008.01933.x

Makridis, P., Martins, S., Vercauteren, T., Driessche, K., Decamp, O., and Dinis, M. T. (2005). Evaluation of Candidate Probiotic Strains for Gilthead Seabream Larvae (*Sparus Aurata*) Using an *In Vivo* Approach. *Lett. Appl. Microbiol.* 40, 274–277. doi: 10.1111/j.1472-765X.2005.01676.x

Ma, Q., Li, L. Y., Le, J. Y., Lu, D. L., Qiao, F., Zhang, M. L., et al. (2018). Dietary Microencapsulated Oil Improves Immune Function and Intestinal Health in

Nile Tilapia Fed With High-Fat Diet. *Aquaculture* 496, 19–29. doi: 10.1016/j.aquaculture.2018.06.080

Martens, T., Heidorn, T., Pukall, R., Simon, M., Tindall, B. J., and Brinkhoff, T. (2006). Reclassification of *Roseobacter Gallaeciensis* Ruiz-Ponte Et Al. 1998 as *Phaeobacter Gallaeciensis* Gen. Nov., Comb. Nov., Description of *Phaeobacter Inhibens* Sp Nov., Reclassification of *Ruegeria Algicola* (Lafay Et Al. 1995) Uchino Et Al. 1999 as *Marinovum Algicola* Gen. Nov., Comb. Nov., and Emended Descriptions of the Genera *Roseobacter*, *Ruegeria* and *Leisingera*. *Int. J. Sys. Evol. Microbiol.* 56, 1293–1304. doi: 10.1099/ijs.0.63724-0

Marti, E., Variatza, E., and Balcázar, J. L. (2014). The Role of Aquatic Ecosystems as Reservoirs of Antibiotic Resistance. *Trends Microbiol.* 22, 1. doi: 10.1016/j.tim.2013.11.001

Maulu, S., Liang, H., Ge, X., Yu, H., Huang, D., Ke, J., et al. (2021a). Effect of Dietary *Clostridium Autoethanogenum* Protein on Growth, Body Composition, Plasma Parameters and Hepatic Genes Expression Related to Growth and AMP/TOR/PI3K Signaling Pathway of the Genetically Improved Farmed Tilapia (GIFT: *Oreochromis Niloticus*) Juveniles. *Anim. Feed Sci. Technol.* 276, 114914. doi: 10.1016/j.anifeedsci.2021.114914

Maulu, S., Liang, H., Ge, X., Yu, H., Huang, D., Ke, J., et al. (2021b). Dietary *Clostridium Autoethanogenum* Protein Modulates Intestinal Absorption, Antioxidant Status, and Immune Response in GIFT (*Oreochromis Niloticus*) Juveniles. *Aquacult. Res.* 52, 5787–5799. doi: 10.1111/are.15454

Melo-Bolivar, J. F., Ruiz Pardo, R. Y., Hume, M. E., and Villamil Diaz, L. ,. M. (2021). Multistrain Probiotics Use in Main Commercially Cultured Freshwater Fish: A Systematic Review of Evidence. *Rev. Aquacult* 13 (4), 1758–1780. doi: 10.1111/raq.12543

Meng, X., Wu, S., Hu, W., Zhu, Z., Yang, G., Zhang, Y., et al. (2021). *Clostridium Butyricum* Improves Immune Responses and Remodels the Intestinal Microbiota of Common Carp (*Cyprinus Carpio* L.). *Aquaculture* 530, 735753. doi: 10.1016/j.aquaculture.2020.735753

Merrifield, D. L., Dimitroglou, A., Foey, A., Davies, S. J., Baker, R. R., Bøgwald, J., et al. (2010). The Current Status and Future Focus of Probiotic and Prebiotic Applications for Salmonids. *Aquaculture* 302, 1–18. doi: 10.1016/j.aquaculture.2010.02.007

Mertes, V., Bekkelund, A. K., Lagos, L., Ciani, E., Colquhoun, D., Hallene-Hox, H., et al. (2021). The Use of Extracellular Membrane Vesicles for Immunization Against Francisellosis in Nile Tilapia (*Oreochromis Niloticus*) and Atlantic Cod (*Gadus Morhua* L.). *Vaccines* 9, 34. doi: 10.3390/vaccines9010034

Midhun, S. J., Neethu, S., Vysakh, A., Arun, D., Radhakrishnan, E. K., and Jyothis, M. (2017). Antibacterial Activity and Probiotic Characterization of Autochthonous Paenibacillus Polymyxa Isolated From Anabas Testudineus (Bloc, 1792). *Microb. Patho*. 113, 403–411. doi: 10.1016/j.micpath.2017.11.019

Mladineo, I., Buselic, I., Hrabar, J., Radonic, I., Vrbatovic, A., Jozic, S., et al. (2016). Autochthonous Bacterial Isolates Successfully Stimulate *In Vitro* Peripheral Blood Leukocytes of the European Sea Bass (*Dicentrarchus Labrax*). *Front. Microbiol.* 7. doi: 10.3389/fmic.2018.01244

Nataraj, B. H., Ali, S. A., Behare, P. V., and Yadav, H. (2020). Postbiotics-Parabiotics; New Horizons in Microbial Biotherapy and Functional Foods. *Microb. Cell Fact.* 19, 168. doi: 10.1186/s2934-020-01426-w

Navarrete, P., Fuentes, P., de la Fuente, L., Barros, L., Magne, F., Opazo, R., et al. (2013). Short-Time Effects of Dietary Soybean Meal and Lactic Acid Bacteria on the Intestinal Morphology and Microbiota of Atlantic Salmon (*Salmo Salar*). *Aquacult. Nutr.* 19 (5), 827–836. doi: 10.1111/anu.12047

Nayak, S. K. (2010). Probiotics and Immunity: A Fish Perspective. *Fish Shellfish Immunol.* 29 (1), 2–14. doi: 10.1016/j.fsi.2010.02.017

Nayak, S. K. (2021). Multifaceted Applications of Probiotic Bacillus Species in Aquaculture With Special Reference to *Bacillus Subtilis*. *Rev. Aquacult.* 13, 862–906. doi: 10.1111/raq.12503

Newaj-Fyzul, A., Al-Harbi, A. H., and Austin, B. (2014). Developments in the Use of Probiotics for Disease Control in Aquaculture. *Aquaculture* 431, 1–11. doi: 10.1016/j.aquaculture.2013.08.026

Nguyen, C. D. H., Amoroso, G., Ventura, T., and Elizur, A. (2020). Assessing the Pyloric Caeca and Distal Gut Microbiota Correlation With Flesh Color in Atlantic Salmon (*Salmo Salar* L. 1758). *Microorganisms* 8, 1244. doi: 10.3390/microorganisms8081244

Nurhidayu, A., Ina-Salwany, M. Y., Daud, H. M., and Harmin, S. A. (2012). Isolation, Screening and Characterization of Potential Probiotics From Farmed Tiger Grouper (Epinephelus Fuscoguttatus). *Afr. J. Microbiol. Res.* 6 (9), 1924–1933. doi: 10.5897/AJMR11.913

O'Brien, A., Sharp, R., Russell, N. J., and Roller, S. (2004). Antarctic Bacteria Inhibit Growth of Food-Borne Microorganisms at Low Temperatures. *FEMS Microbiol. Ecol.* 48 (2), 157–167. doi: 10.1016/j.femsec.2004.01.001

Offret, C., Desriac, F., Le Chevalier, P., Mounier, J., Jegou, C., and Fleury, Y. (2016). Spotlight on Antimicrobial Metabolites From the Marine Bacteria *Pseudoalteromonas*: Chemodiversity and Ecological Significance. *Mar. Drugs* 14 (7), 26. doi: 10.3390/md14070129

Osungbemiro, N. R., Belloolusoji, O. A., and Oladipupo, M. (2018). "Effects of Probiotic Pseudomonas Fluorescens on the Growth Performance, Immune Modulation, and Histopathology of African Catfish (Clarias Gariepinus). ICAND 2018," in *International Conference on Animal Diseases and Nutrition*(New York, USA).

Ottesen, O. H., and Olafsen, J. A. (2000). Effects on Survival and Mucous Cell Proliferation of Atlantic Halibut, *Hippoglossus Hippoglossus* L., Larvae Following Microflora Manipulation. *Aquaculture* 187, 225–238. doi: 10.1016/S0044-8486(00)00314-8

Palleroni, N. J. (1992). "Introduction to the Family Pseudomonadaceae," in *The Prokaryotes, 2nd ed* (New York Dordrecht London: Springer Heidelberg), 3071–3085. doi: 10.1007/978-3-642-30194-0

Pan, X., Wu, T., Song, Z., Tang, H., and Zhao, Z. (2008). Immune Responses and Enhanced Disease Resistance in Chinese Drum, *Miichthys Miiuy* (Basilewsky), After Oral Administration of Live or Dead Cells of *Clostridium Butyricum* CB2. *J. Fish Dis.* 31, 679–686. doi: 10.1111/j.1365-2761.2008.00955.x

Papaleo, M. C., Fondi, M., Maida, I., Perrin, E., Lo Giudice, A., Michaud, L., et al. (2012). Sponge-Associated Microbial Antarctic Communities Exhibiting Antimicrobial Activity Against *Burkholderia Cepacia* Complex Bacteria. *Biotechnol. Adv.* 30 (1), 272–293. doi: 10.1016/j-biotechadv.2011.06.011

Peixoto, M. J., Domingues, A., Batista, S., Goncalves, J. F. M., Gomes, A. M., Cunha, S., et al. (2018). Physiopathological Responses of Sole (*Solea Senegalensis*) Subjected to Bacterial Infection and Handling Stress After Probiotic Treatment With Autochthonous Bacteria. *Fish Shellfish Immunol.* 83, 348–358. doi: 10.1016/j.fsi.2018.09.045

Pérez-Pascual, D., Estellé, J., Dutto, G., Rodde, C., Bernardet, J.-F., Marchand, Y., et al. (2020). Growth Performance and Adaptability of European Sea Bass (*Dicentrarchus Labrax*) Gut Microbiota to Alternative Diets Free of Fish Products. *Microorganisms* 8, 18. doi: 10.3390/microorganisms8091346

Piazzon, M. C., Naya-Catala, F., Simo-Mirabet, P., Picard-Sanchez, A., Roig, F. J., Calduch-Giner, J. A., et al. (2019). Sex, Age, and Bacteria: How the Intestinal Microbiota is Modulated in a Protandrous Hermaphrodite Fish. *Front. Microbiol.* 10. doi: 10.3389/fmicb.2019.02512

Pieters, N., Brunt, J., Austin, B., and Lyndon, A. R. (2008). Efficacy of in-Feed Probiotics Against *Aeromonas Bestiarum* and *Ichthyophthirius Multifiliis* Skin Infections in Rainbow Trout (*Oncorhynchus Mykiss*, Walbaum). *J. Appl. Microbiol.* 105, 723–732. doi: 10.1111/j.1365-2672.2008.03817.x

Pietsch, C. (2020). Risk Assessment for Mycotoxin Contamination in Fish Feeds in Europe. *Mycotoxin Res.* 36, 41–62. doi: 10.1007/s12550-019-00368-6

Planas, M., Pérez-Lorenzo, M., Hjelm, M., Gram, L., Uglenes Fiksdal, I., Bergh, Ø., et al. (2004). Probiotic Effect *In Vivo* of *Roseobacter* Strain 27-4 Against *Vibrio* (*Listonella*) *Anguillarum* Infections in Turbot (*Scophthalmus Maximus* L.) Larvae). *Aquaculture* 255, 323–333. doi: 10.1016/j.aquaculture.2005.11.039

Poolsawat, L., Li, X., He, M., Ji, D., and Leng, X. (2020). *Clostridium Butyricum* as Probiotic for Promoting Growth Performance, Feed Utilization, Gut Health and Microbiota Community of Tilapia (*Oreochromis Niloticus* X *O. Aureus*). *Aquacult. Nutr.* 26, 657–670. doi: 10.1111/anu.13025

Porsby, C. H., Nielsen, K. F., and Gram, L. (2008). *Phaeobacter* and *Ruegeria* Species of the *Roseobacter* Clade Colonize Separate Niches in a Danish Turbot (*Scophthalmus Maximus*)-Rearing Farm and Antagonize *Vibrio Anguillarum* Under Different Growth Conditions. *Appl. Environ. Microbiol.* 74 (23), 7356–7364. doi: 10.1128/AEM.01738-08

Prado, S., Barja, J. L., Luzardo, A., Dubert, J., and Blanco, J. (2020). Encapsulation of Live Marine Bacteria for Use in Aquaculture Facilities and Process Evaluation Using Response Surface Methodology. *Appl. Microbiol. Biotechnol.* 104 (5), 1993–2006. doi: 10.1007/s00253-019-10332-0

Prado, S., Romalde, J. L., and Barja, J. L. (2010). Review of Probiotics for Use in Bivalve Hatcheries. *Vet. Microbiol.* 145, 187–197. doi: 10.1016/j.vetmic.2010.08.021

Prol, M. J., Bruhn, J. B., Pintado, J., and Gram, L. (2009). Real-Time PCR Detection and Quantification of Fish Probiotic *Phaeobacter* Strain 27-4 and Fish Pathogenic *Vibrio* in Microalgae, Rotifer, *Artemia* and First Feeding Turbot (*Psetta Maxima*) Larvae. *J. Appl. Microbiol.* 106 (4), 1292–1303. doi: 10.1111/j.1365-2672.2008.04096.x

Prol-García, M. J., and Pintado, J. (2013). Effectiveness of Probiotic *Phaeobacter* Bacteria Grown in Biofilters Against *Vibrio Anguillarum* Infections in the Rearing of Turbot (*Psetta Maxima*) Larvae. *Mar. Biotechnol.* 15, 726–738. doi: 10.1007/s1026-013-9521-4

Qi, X., Xue, M. Y., Cui, H. B., Yang, K. C., Song, K. G., Zha, J. W., et al. (2020). Antimicrobial Activity of *Pseudomonas Monteilii* JK-1 Isolated From Fish Gut and its Major Metabolite, 1-Hydroxyphenazine, Against *Aeromonas Hydrophila*. *Aquaculture* 526, 735366. doi: 10.1016/j.aquaculture.2020.735366

Rahman, F., Meryandini, A., and Rusmana, I. (2016). Substrates Break Down and Agarase Activity of *Vibrio* Spp. As Probiotics Candidate for Abalon. *Eur. J. Adv. Res. Biol. Life Sci.* 4 (3), 14–22.

Ran, C., Li, Y., Ma, X., Xie, Y., Xie, M., Zhang, Y., et al. (2021). Interactions Between Commensal Bacteria and Viral Infection: Insight for Viral Disease Control in Farmed Animals. *Sci. China Life Sci.* 64, 1437–1448. doi: 10.1007/s1111427-020-1721-5

Rasmussen, B. B., Klatzis, P. G., Middelboe, M., and Gram, L. (2019). Combining Probiotic *Phaeobacter Inhibens* DSM and Broad-Host-Range Vibriophage KVP40 Against Fish Pathogenic Vibrios. *Aquaculture* 513, 734415. doi: 10.1016/aquaculture.2019.734415

Richards, G. P., Watson, M. A., Needleman, D. S., Uknalis, J., Boyd, E. F., and Fay, J. P. (2017). Mechanisms for *Pseudoalteromonas Piscicida*-Induced Killing of Vibrios and Other Bacterial Pathogens. *Appl. Environ. Microbiol.* 83 (11), e00175–e00117. doi: 10.1128/AEM.00175-17

Rimoldi, S., Torrecillas, S., Montero, D., Gini, E., Makol, A., Valdenegro, V., et al. (2020). Assessment of Dietary Supplementation With Galactomannan Oligosaccharides and Phytogenics on Gut Microbiota of European Sea Bass (*Dicentrarchus Labrax*) Fed Low Fishmeal and Fish Oil Based Diet. *Pos One* 15 (4), e0231494. doi: 10.1371/journal.pone.0231494

Ringø, E. (1993). The Effect of Chromic Oxide (Cr_2O_3) on Aerobic Bacterial Populations Associated With the Intestinal Mucosa of Arctic Charr, *Salvelinus Alpinus* (L). *Can. J. Microbiol.* 39 (12), 1169–1173. doi: 10.1139/m93-177

Ringø, E. (1999). Does *Carnobacterium Divergens* Isolated From Atlantic Salmon (*Salmo Salar* L.) Colonise the Gut of Early Developing Turbot (*Scophthalmus Maximus* L.) Larvae? *Aquacult. Res.* 30 (3), 229–232. doi: 10.1046/j.1365-2109.1999.00269.x

Ringø, E. (2020). Probiotics in Shellfish Aquaculture. *Aquacult. Fish.* 5 (1), 1–27. doi: 10.1016/j.aaf.2019.12.001

Ringø, E., Birkbeck, T. H., Munro, P. D., Vadstein, O., and Hjelmeland, K. (1996). The Effect of Early Exposure to *Vibrio Pelagius* on the Aerobic Bacterial Flora of Turbot, *Scophthalmus Maximus* (L.) Larvae. *J. Appl. Bacteriol.* 81 (2), 207–211. doi: 10.1111/j.1365-2672.1996.tb04502.x

Ringø, E., Hoseinifar, S. H., Ghosh, K., van Doan, H., Beck, B. R., and Song, S. K. (2018). Lactic Acid Bacteria in Finfish – an Update. *Front. Microbiol.* 9. doi: 10.3389/fmicb.2018.01818

Ringø, E., Olsen, R. E., Øverli, Ø., and Løvik, F. (1997). Effect of Dominance Hierarchy Formation on Aerobic Microbiota Associated With Epithelial Mucosa of Subordinate and Dominant Individuals of Arctic Charr, *Salvelinus Alpinus* (L.). *Aquacult. Res.* 28, 901–904. doi: 10.1111/j.1365-2109.1997.tb01014.x

Ringø, E., Sperstad, S., Kraugerud, O. F., and Krogdahl, Å. (2008). Use of 16S rRNA Gene Sequencing Analysis to Characterise Culturable Intestinal Bacteria in Atlantic Salmon (*Salmo Salar* L.) Fed Diets With non-Starch Polysaccharides From Soy and Cellulose. *Aquacult. Res.* 39, 1087–1100. doi: 10.1111/j.1365-2109.2008.01972.x

Ringø, E., Sperstad, S., Myklebust, R., Mayhew, T. M., Mjelde, A., Melle, W., et al. (2006b). The Effect of Dietary Krill Supplementation on Epithelium-Associated Bacteria in the Hindgut of Atlantic Salmon (*Salmo Salar* L.). A Microbial and Electron Microscopical Study. *Aquacult. Res.* 37, 1644–1653. doi: 10.1111/j.1365-2109.2006.01611.x

Ringø, E., Sperstad, S., Myklebust, R., Refstie, S., and Krogdahl, Å. (2006a). Characterisation of the Microbiota Associated With the Intestine of Atlantic Cod (*Gadus Morhua* L.). The Effect of Fish Meal, Soybean Meal and a Bioprocessed Soybean Meal. *Aquaculture* 261, 829–841. doi: 10.1016/j.aquaculture.2006.06.030

Ringø, E., Stenberg, E., and Strøm, A. R. (1984). Amino Acid and Lactate Catabolism in Trimethylamine-Oxide Respiration of *Alteromonas Putrefaciens* NCMB 1735. *Appl. Environ. Microbiol.* 47, 1084–1089. doi: 10.1128/aem.47.5.1084-1089.1984

Ringø, E., and Vadstein, O. (1998). Colonization of *Vibrio Pelagius* and *Aeromonas Caviae* in Early Developing Turbot, *Scophthalmus Maximus* (L.) Larvae. *J. Appl. Microbiol.* 84, 227–233. doi: 10.1046/j.1365-2672.1998.00333.x

Ringø, E., van Doan, H., Lee, S. H., Soltani, M., Hoseinifar, S. H., Ramasamy, H., et al. (2020a). Probiotics, Lactic Acid Bacteria and Bacilli: Interesting Supplementation for Aquaculture. *J. Appl. Microbiol.* 129, 116–136. doi: 10.1111/jam.14628

Ringø, E., van Doan, H., Lee, S., and Song, S. K. (2020b). Lactic Acid Bacteria in Shellfish: Possibilities and Challenges. *Rev. Fish. Sci. Aquacult.* 28 (2), 139–169. doi: 10.1080/23308249.2019.1683151

Ringø, E., Zhou, Z., Gonzalez Vecino, J. L., Wadsworth, S., Romero, J., Krogdahl, Å., et al. (2016). Effects of Dietary Components on the Gut Microbiota of Aquatic Animals: A Never-Ending Story? *Aquacult. Nutr.* 22, 219–282. doi: 10.1111/anu12346

Riviere, A., Selak, M., Lantin, D., Leroy, F., and De Vuyst, L. (2016). Bifidobacteria and Butyrate-Producing Colon Bacteria: Importance and Strategies for Their Stimulation in the Human Gut. *Front. Microbiol.* 7. doi: 10.3389/fmicb.2016.00979

Rosas-Ledesma, P., Leon-Rubio, J. M., Alarcon, F. J., Morinigo, M. A., and Balebona, M. C. (2012). Calcium Alginate Capsules for Oral Administration of Fish Probiotic Bacteria: Assessment of Optimal Conditions for Encapsulation. *Aquacult. Res.* 43 (1), 106–116. doi: 10.1111/j.1365-2109.2011.02809.x

Royan, S., Parulekar, C., and Mavinkurve, S. (1999). Exopolysaccharides of *Pseudomonas Mendocina* P2d. *Lett. Appl. Microbiol.* 29 (5), 342–346. doi: 10.1046/j.1472-765X.1999.00638

Rud, I., Kolarevic, J., Holan, A. B., Berget, I., Calabrese, S., and Terjesen, B. F. (2017). Deep-Sequencing of the Bacterial Microbiota in Commercial-Scale Recirculating and Semi-Closed Aquaculture Systems for Atlantic Salmon Post-Smolt Production. *Aquacult. Eng.* 78, 50–62. doi: 10.1016/j.aquaeng.2016.10.003

Sáenz de Rodrigáñez, M. A., Díaz-Rosales, P., Chabrillón, M., Smidt, H., Arijo, S., Leon-Rubio, J. M., et al. (2009). Effect of Dietary Administration of Probiotics on Growth and Intestine Functionality of Juvenile Senegalese Sole (*Sole Senegalensis*, Kaup 1858). *Aquacult. Nutr.* 15, 177–185. doi: 10.1111/j.1365-2095.2008.00581.x

Saenz, J. S., Marques, T. V., Barone, R. S. C., Cyrino, J. E. P., Kublik, S., Nesme, J., et al. (2019). Oral Administration of Antibiotics Increased the Potential Mobility of Bacterial Resistant Genes in the Gut of Fish *Piaractus Mesopotamicus*. *Microbiome* 7, 14. doi: 10.1186/s40168-019-0632-7

Saettone, V., Biasato, I., Radice, E., Schiavone, A., Bergero, D., and Meineri, G. (2020). State-Of-the-Art of the Nutritional Alternatives to the Use of Antibiotics in Human and Monogastric Animals. *Animals* 10, 2199. doi: 10.3390/ani10122199

Sahandi, J., Jafaryan, H., Soltani, M., and Ebrahimi, P. (2017). Enhancement of Growth Performance and Haematological Changes in Rainbow Trout (*Oncorhynchus Mykiss*) Alevins Fed With *Bifidobacterium* Bacteria. *J. Fish.* 5 (1), 439–444. doi: 10.1017/jfish.v5i1.2017.152

Sahandi, J., Jafaryan, H., Soltani, M., and Ebrahimi, P. (2019). The Use of Two *Bifidobacterium* Strains Enhanced Growth Performance and Nutrient Utilisation of Rainbow Trout (*Oncorhynchus Mykiss*) Fry. *Prob. Antimicrob. Prot.* 11, 966–972. doi: 10.1007/s12602-018-9455-2

Sakai, M., Yoshida, T., Atsuta, S., and Kobayashi, M. (1995). Enhancement of Resistance to Vibriosis in Rainbow Trout, *Oncorhynchus Mykiss* (Walbaum), by Oral Administration of *Clostridium Butyricum* Bacterin. *J. Fish Dis.* 18, 187–190. doi: 10.1111/j.1365-2761.1995.tb00276.x

Salinas, I., Diaz-Rosales, P., Cuesta, A., Meseguer, J., Chabrillón, M., Morinigo, M. A., et al. (2006). Effect of Heat-Inactivated Fish and non-Fish Derived Probiotics on the Innate Immune Parameters of a Teleost Fish (*Sparus Aurata* L.). *Vet. Immunol. Immunopathol.* 111 (3-4), 279–286. doi: 10.1016/j.vetimm.2006.01.020

Salyers, A. A., Gupta, A., and Wang, Y. (2004). Human Intestinal Bacteria as Reservoirs for Antibiotic Resistance Genes. *Trends Microbiol.* 14 (9), 412–416. doi: 10.1016/j.tim.2004.07.004

Sankar, H., Philip, B., Philip, R., and Singh, I. S. B. (2017). Effect of Probiotics on Digestive Enzyme Activities and Growth of Cichlids, *Etroplus Suratensis* (Pearl Spot) and *Oreochromis Mossambicus* (Tilapia). *Aquacult. Nutr.* 23 (4), 852–864. doi: 10.1111/anu.12452

Satomi, M., Vogel, B. F., Gram, L., and Venkateswaran, K. (2006). *Shewanella Putrefaciens* Sp. Nov and *Shewanella Morhuae* Sp. Nov., Isolated From Marine Fish of the Baltic Sea. *Int. J. Sys. Evol. Microbiol.* 56, 243–249. doi: 10.1099/ijs.0.63931-0

Satomi, M., Vogel, B. F., Venkateswaran, K., and Gram, L. (2007). Description of *Shewanella Glacialipiscicola* Sp. Nov and *Shewanella Algidipiscicola* Sp. Nov., Isolated From Marine Fish of the Danish Baltic Sea, and Proposal That *Shewanella Affinis* is a Later Heterotypic Synonym of *Shewanella Colwelliana*. *Int. J. Sys. Evol. Microbiol.* 57, 347–352. doi: 10.1099/ijs.0.64708-0

Schaeck, M., Duchateau, L., Van den Broeck, W., Van Trappen, S., De Vos, P., Coulombet, C., et al. (2016). *Vibrio Lentus* Protects Gnotobiotic Sea Bass (*Dicentrarchus Labrax* L.) Larvae Against Challenge With *Vibrio Harveyi*. *Vet. Microbiol.* 185, 41–48. doi: 10.1016/j.vetmic.2016.01.024

Schaeck, M., Reyes-Lopez, F. E., Vallejos-Vidal, E., Van Cleemput, J., Duchateau, L., Van den Broeck, W., et al. (2017). Cellular and Transcriptomic Response to Treatment With the Probiotic Candidate *Vibrio Lentus* in Gnotobiotic Sea Bass (*Dicentrarchus Labrax*) Larvae. *Fish Shellfish Immunol.* 63, 147–156. doi: 10.1016/j.fsi.2017.01.028

Schmidt, V., Gomez-Chiarri, M., Roy, C., Smith, K., and Amaral-Zettler, L. (2017). Subtle Microbiome Manipulation Using Probiotics Reduces Antibiotic-Associated Mortality in Fish. *MSystems* 2 (6), e00133–e00117. doi: 10.1128/mSystems.00133-17

Sedlacek, I., Stankova, E., and Svec, P. (2016). Composition of Cultivable Enteric Bacteria From the Intestine of Antarctic Fish (Family Nototheniidae). *Czech J. Anim. Sci.* 61 (3), 127–132. doi: 10.17221/8785-CJAS

Seoane, P., Tapia-Paniagua, S. T., Bautista, R., Alcaide, E., Esteve, C., Martinez-Manzanares, E., et al. (2019). TarSynFlow, a Workflow for Bacterial Genome Comparisons That Revealed Genes Putatively Involved in the Probiotic Character of *Shewanella Putrefaciens* Strain Pdp11. *PeerJ* 7, e6526. doi: 10.7717/peerj.6526

Shah, N. P. (1997). Isolation and Enumeration of Bifidobacteria in Fermented Milk Products: A Review. *Milchwissenschaft* 52, 71–76.

Shamsuzzaman, M. M., and Kumar, B. T. (2012). Aqua Chemicals in Shrimp Farm: A Study From South-West Coast of Bangladesh. *Egyptian J. Aquat. Res.* 38, 275–285. doi: 10.1016/j.ejar.2012.12.08

Sharifuzzaman, S. M., Abbass, A., Tinsley, J. W., and Austin, B. (2011). Subcellular Components of Probiotics *Kocuria* SM1 and *Rhodococcus* SM2 Induce Protective Immunity in Rainbow Trout (*Oncorhynchus Mykiss*, Walbaum) Against *Vibrio Anguillarum*. *Fish Shellfish Immunol.* 30, 347–353. doi: 10.1016/j.fsi.2010.11.005

Sharifuzzaman, S. M., Al-Harbi, A. H., and Austin, B. (2014). Characteristics of Growth, Digestive System Functionality, and Stress Factors of Rainbow Trout Fed Probiotics *Kocuria* SM1 and *Rhodococcus* Sm2. *Aquaculture* 418, 55–61. doi: 10.1016/j.aquaculture.2013.10.006

Sharifuzzaman, S. M., and Austin, B. (2010a). Development of Protection in Rainbow Trout (*Oncorhynchus Mykiss*, Walbaum) to *Vibrio Anguillarum* Following Use of the Probiotic *Kocuria* Sm1. *Fish Shellfish Immunol.* 29, 212–216. doi: 10.1016/j.fsi.2010.03.008

Sharifuzzaman, S. M., and Austin, B. (2010b). *Kocuria* SM1 Controls Vibriosis in Rainbow Trout (*Oncorhynchus Mykiss*, Walbaum). *J. Appl. Microbiol.* 108, 2162–2170. doi: 10.1111/j.1365-2672.2009.04618.x

Sharifuzzaman, S. M., Rahman, H., Austin, D. A., and Austin, B. (2018). Properties of Probiotics *Kocuria* SM1 and *Rhodococcus* SM2 Isolated From Fish Guts. *Prob. Antimicrob. Prot.* 10 (3), 534–542. doi: 10.1007/s12601-017-9290-x

Silby, M. W., Winstanley, C., Godfrey, S. A. C., Levy, S. B., and Jackson, R. W. (2011). *Pseudomonas* Genomes: Diverse and Adaptable. *FEMS Microbiol. Rev.* 35 (4), 652–680. doi: 10.1111/j.1574-6976.2011.00269.x

Skjermo, J., Bakke, I., Dahle, S. W., and Vadstein, O. (2015). Probiotic Strains Introduced Through Live Feed and Rearing Water Have Low Colonizing Success in Developing Atlantic Cod Larvae. *Aquaculture* 438, 17–23. doi: 10.1016/j.aquaculture.2014.12.027

Smith, P., and Davey, S. (1993). Evidence for the Competitive Exclusion of *Aeromonas Salmonicida* From Fish With Stress-Inducible Furunculosis by a Fluorescent Pseudomonad. *J. Fish Dis.* 16 (5), 521–554. doi: 10.1111/j.1365-2761.1993.tb00888.x

Sneath, P. H. A., and Jones, D. (1976). *Brochothrix*, a New Genus Tentatively Placed in the Family Lactobacillaceae. *J. Sys. Bacteriol.* 26, 102–104. doi: 10.1099/00207713-26-2-102

Soltani, M., Ghosh, K., Hoseinifar, S. H., Kumar, V., Lymbery, A., Roy, S., et al. (2019). Genus *Bacillus*, Promising Probiotics in Aquaculture: Aquatic Animal Origin, Bio-Active Components, Bioremediation in Fish and Shellfish. *Rev. Fish. Sci. Aquacult.* 27 (3), 331–379. doi: 10.1080/23308249.2019.1597010

Song, W., Li, L. Z., Huang, H. L., Jiang, K. J., Zhang, F. Y., Chen, X. Z., et al. (2016). The Gut Microbial Community of Antarctic Fish Detected by 16S rRNA Gene Sequence Analysis. *BioMed. Res. Inter.* 2016, 3241529. doi: 10.1155/2016/3241529

Song, Z.-F., Wu, T.-X., Cai, L.-S., Zhang, L.-J., and Zheng, X.-D. (2006). Effects of Dietary Supplementation With *Clostridium Butyricum* on the Growth Performance and Humoral Immune Response in *Miichtys Miiuy*. *J. Zhejiang Univ. Sci. B* 7, 596–602. doi: 10.1631/jzus.2006.B0596

Stackebrandt, E., Koch, C., Gvozdiak, O., and Schumann, P. (1995). Taxonomic Dissection of the Genus *Micrococcus: Kocuria* Gen. Nov., *Nesterenkonia* Gen. Nov., *Kytococcus* Gen. Nov., *Dermacoccus* Gen. Nov., and *Micrococcus* Cohn 1872 Gen. Emend. *Int. J. Syst. Bacteriol.* 45 (4), 682–693. doi: 10.1099/00207713-45-4-682

Strom-Bestor, M., and Wiklund, T. (2011). Inhibitory Activity of *Pseudomonas* Sp. On *Flavobacterium Psychrophilum In Vitro*. *J. Fish Dis.* 34, 255–264. doi: 10.1111/j.1365-2761.2010.01232.x

Sun, Y. Z., Xia, H. Q., Yang, H. L., Wang, Y. L., and Zou, W. C. (2014). TLR2 Signaling may Play a Key Role in the Probiotic Modulation of Intestinal Microbiota in Grouper *Epinephelus Coioides*. *Aquaculture* 430, 50–56. doi: 10.1016/j.aquaculture.2014.03.042

Sun, Y. Z., Yang, H. L., Ma, R. L., Zhang, C. X., and Lin, W. Y. (2011). Effect of Dietary Administration of *Psychrobacter* sp. on the growth, feed utilization, digestive enzymes and immune responses of grouper *Epinephelus coioides*. *Aquacult. Nutr.* 17, e733–e740. doi: 10.1111/j.1365-2095.2010.00837.x

Suryaningsih, W., Maulana, R., Istiqomah, I., and Isnansetyo, A. (2021). *In Vitro* Adhesion of *Bacillus* Sp. And *Enterobacter* Sp. Probiotics on Intestinal Epithelial Cells of Red Tilapia (*Oreochromis* Sp.) and the Application Effects on the Fish Growth and Survival Rate. *IOP Conf. Ser. Earth Environ. Sci.* 919, 12056. doi: 10.1088/1755-1315/919/1/012056

Takeuchi, M., and Hatano, K. (1998). Proposal of Six New Species in the Genus Microbacterium and Transfer of Flavobacterium Marinotypicum ZoBell and Upham to the Genus Microbacterium as Microbacterium Maritypicum Comb. Nov.. *Int. J. Syst. Bacteriol.* 48, 973–82. doi: 10.1099/00207713-48-973

Tamboli, C. P., Neut, C., Desreumaux, P., and Colombel, J. F. (2004). Dysbiosis as a Prerequisite for IBD. *Gut* 53 (7), 1057.

Tandberg, J. I., Lagos, L., Kashulin, A., Sørum, H., and Winter-Larsen, H. C. (2019). Bacterial Membrane Vesicles as Vaccines in Aquaculture. *Fish Shellfish Immunol.* 91, 425–425 (abstract). doi: 10.1016/j.fsi.2019.04.163

Tang, K., Huang, H., Jiao, N., and Wu, C. H. (2010). Phylogenomic Analysis of Marine Roseobacters. *PloS One* 5 (7), e11604. doi: 10.1371/journal.pone.0011604

Tan, P., Wu, X., Zhu, W., Lou, B., Chen, R., and Wang, L. (2020). Effect of Tributyrin Supplementation in High-Soya Bean Meal Diet on Growth Performance, Body Composition, Intestine Morphology and Microbiota of Juvenile Yellow Drum (*Nibea Albiflora*). *Aquacult. Res.* 51, 2004–2019. doi: 10.1111/are.14552

Tapia-Panagia, S. T., Fumanal, M., Anguis, V., Fernández-Díaz, C., Alarcón, F. J., Moriñigo, M. A., et al. (2019). Modulation of Intestinal Microbiota in *Solea Senegalensis* Fed Low Dietary Level of *Ulva Ohnoi*. *Front. Microbiol.* 10, 171. doi: 10.3389/fmicb.2019.00171

Tapia-Paniagua, S. T., Chabrillón, M., Diaz-Rosales, P., de la Banda, I. G., Lobo, C., Balebona, M. C., et al. (2010). Intestinal Microbiota Diversity of the Flat Fish Solea Senegalensis (Kaup, 1858) Following Probiotic Administration. *Microb. Ecol.* 60 (2), 310–319. doi: 10.1007/s00248-010-9680-z

Tapia-Paniagua, S. T., Díaz-Rosales, P., León-Rubio, J. M., García de la Banda, I., Lobo, C., Alarcón, F. J., et al. (2012). Use of the Probiotic *Shewanella Putrefaciens* Pdp11 on the Culture of Senegalese Sole (*Solea Senegalensis* Kaup 1858) and Gilthead Seabream (*Sparus Aurata* L.). *Aquacult. Int.* 20, 1025–1039. doi: 10.1007/s10499-012-9509-5

Tapia-Paniagua, S. T., Lobo, C., Moreno-Ventas, X., de la Banda, I. G., Moriñigo, M. A., and Balebona, M. C. (2014a). Probiotic Supplementation Influences the Diversity of the Intestinal Microbiota During Early Stages of Farmed Senegalese Sole (*Solea Senegalensis*, Kaup 1858). *Mar. Biotechnol.* 16, 716–728. doi: 10.1007/s10126-014-9588-6

Tapia-Paniagua, S. T., Vidal, S., Lobo, C., Prieto-Álamo, M. J., Jurado, J., Cordero, H., et al. (2014b). The Treatment With the Probiotic *Shewanella Putrefaciens* Pdp11 of Specimens of *Solea Senegalensis* Exposed to High Stocking Densities to Enhance Their Resistance to Disease. *Fish Shellfish Immunol.* 41 (2), 209–221. doi: 10.1016/j.fsi.2014.08.019

Taverniti, V., and Guglielmetti, S. (2011). The Immunomodulatory Properties of Probiotic Microorganism Beyond Their Viability (Ghost Probiotics: Proposal of Paraprobiotic Concept). *Genes Nutr.* 6 (3), 261–271. doi: 10.1007/s12263-011-0218-x

Teame, T., Wang, A., Xie, M., Zhang, Z., Yang, Y., Ding, Q., et al. (2020). Paraprobiotics and Postbiotics of Probiotic Lactobacilli, Their Positive Effects on the Host and Action Mechanisms: A Review. *Front. Nutr.* 7. doi: 10.3389/fnut.2020.570144

Terova, G., Rimoldi, S., Ascione, C., Gini, E., Ceccotti, C., and Gasco, L. (2019). Rainbow Trout (*Oncorhynchus Mykiss*) Gut Microbiota is Modulated by Insect Meal From *Hermetia Illucens* Prepupae in the Diet. *Rev. Fish Biol. Fish.* 29, 465–486. doi: 10.1007/s11160-019-09558-y

Tobar, I., Arancibia, S., Torres, C., Vera, V., Soto, P., Carrasco, C., et al. (2015). Successive Oral Immunizations Against *Piscirickettsia Salmonis* and Infectious Salmon Anemia Virus are Required to Maintain a Long-Term Protection in Farmed Salmonids. *Front. Immunol.* 6. doi: 10.3389/fimmu.2015.00244

Tran, N. T., Li, Z., Ma, H., Zhang, Y., Zheng, H., Gong, Y., et al. (2020). *Clostridium Butyricum*: A Promising Probiotic Confers Positive Health Benefits in Aquatic Animals. *Rev. Aquacult.* 12, 2573–2589. doi: 10.1111/raq.12459

Turchini, G. M., Francis, D. S., Du, Z.-Y., Olsen, R. E., Ringø, E., and Tocher, D. R. (2022). ""Chapter 5. The Lipids"," in *Fish Nutrition, 4th Edition*. Ed. R. Hardy (125 London Wall, London EC2Y 5AS, United Kingdom: Elsevier), 244. ISBN: 978-0-12-819587-1

Turroni, F., Ventura, M., Buttó, L. F., Duranti, S., O`Toole, R. W., O`Connel Motherway, M., et al. (2014). Molecular Dialogue Between the Human Gut Microbiota and the Host: A *Lactobacillus* and *Bifidobacterium* Perspective. *Cell. Mol. Life Sci.* 71, 183–203. doi: 10.1007/s00018-013-1318-0

Van Doan, H., Hoseinifar, S. H., Ringø, E., Esteban, M.Á., Dadar, M., Dawood, M. A. O., et al. (2020). Host-Associated Probiotics: A Key Factor in Sustainable Aquaculture. *Rev. Fish. Sci. Aquacult.* 28 (1), 16–42. doi: 10.1080/23308249.2019.1643288

van Doan, H., Soltani, M., and Ringø, E. (2021). *In Vitro* Antagonistic Effect and *In Vivo* Protective Efficacy of Gram-Positive Probiotics Versus Gram-Negative Bacterial Pathogens in Finfish and Shellfish. *Aquaculture* 538, 736581. doi: 10.1016/j.aquaculture.2021.736581

Varela, J. L., Ruíz-Jarabo, I., Vargas-Chacoff, L., Arijo, S., Leon-Rubio, J. M., Garcia-Millan, I., et al. (2010). Dietary Administration of Probiotic Pdp11 Promotes Growth and Improves Stress Tolerance to High Stocking Density in Gilthead Seabream *Sparus Auratus*. *Aquaculture* 309, 265–271. doi: 10.1016/j.aquaculture.2010.09.029

Vargas-Albores, F., Martínez-Córdova, L. R., Hernández-Mendoza, A., Cicala, F., Lago-Lestón, A., and Martínez-Porchas, M. (2021). Therapeutic Modulation of Fish Gut Microbiota, a Feasible Strategy for Aquaculture? *Aquaculture* 544, 737050. doi: 10.1016/j.aquaculture.2021.737050

Venkataramana, K., Padmavali, P., Ritu, V., Adnan, B. B., Vinod, K., Maheshwar, R. K., et al. (2016). Emerging Bacterial Infection: Identification and Clinical Significance of *Kocuria* Species. *Cureus* 8 (8), e731. doi: 10.7759/cureus.731

Verschuere, L., Rombaut, G., Sorgeloos, P., and Verstraete, W. (2000). Probiotic Bacteria as Biological Control Agents in Aquaculture. *Microbiol. Mol. Biol. Rev.* 64 (4), 655–671. doi: 10.1128/MMBR.64.4.655-671.2000

Vidal, S., Tapia-Paniagua, S. T., Morinigo, J. M., Lobo, C., de la Banda, I. G., Balebona, M. D., et al. (2016). Effects on Intestinal Microbiota and Immune Genes of *Solea Senegalensis* After Suspension of the Administration of *Shewanella Putrefaciens* Pdp11. *Fish Shellfish Immunol.* 58, 274–283. doi: 10.1016/j.fsi.2016.09.010

Vieco-Saiz, N., Belguesmia, Y., Raspoet, R., Auclair, E., Gancel, F., Kempf, I., et al. (2019). Benefits and Inputs From Lactic Acid Bacteria and Their Bacteriocins as Alternatives to Antibiotic Growth Promoters During Food-Animal Production. *Front. Microbiol.* 10. doi: 10.3389/fmicb.2019.00057

Villamil, L., Figueras, A., Planas, M., and Novoa, B. (2010). *Pediococcus Acidilactici* in the Culture of Turbot (*Psetta Maxima*) Larvae, Administration Pathways. *Aquaculture* 307, 83–88. doi: 10.1016/j.aquaculture.2010.07.004

Vine, N. G. (2004). *Towards the Development of a Protocol for the Selection of Probiotics in Marine Fish Larviculture. PhD Thesis* (South Africa: Rhodes University, Grahamstown), 222.

Vine, N. G., Leukes, W. D., and Kaiser, H. (2006). Probiotics in Marine Larviculture. *FEMS Microbiol. Rev.* 30, 404–427. doi: 10.1111/j.1574-6976.2006.00017.x

Vlkova, E., Kalous, L., Bunesova, V., Rylkova, K., Svetlikova, R., and Rada, V. (2012). Occurrence of Bifidobacteria and Lactobacilli in Digestive Tract of Some Freshwater Fishes. *Biologia* 67 (2), 411–416. doi: 10.2478/s11756-012-0017-x

Wagner-Döbler, I., and Biebl, H. (2006). Environmental Biology of the Marine *Roseobacter* Lineage. *Ann. Rev. Microbiol.* 60, 255–280. doi: 10.1146/annurev.micro.60.080805.142115

Wang, Y. (2011). Use of Probiotics *Bacillus Coagulans*, *Rhodopseudomonas Palustris* and *Lactobacillus Acidophilus* as Growth Promoters in Grass Carp (*Ctenopharyngodon Idella*) Fingerlings. *Aquacult. Nutr.* 17 (2), e372–e378. doi: 10.1111/j.1365-2095.2010.00771.x

Wang, R.-F., An, X.-P., Wang, Y., Qi, J.-W., Zhang, J., Liu, Y.-H., et al. (2020b). Effects of Polysaccharide From Fermented Wheat Bran on Growth Performance, Muscle Composition, Digestive Enzyme Activities and Intestinal Microbiota in Juvenile Common Carp. *Aquacult. Nutr.* 26 (4), 1096–1107. doi: 10.1111/anu.13067

Wang, C., Chuprom, J., Wang, Y., and Fu, L. (2019a). Beneficial Bacteria for Aquaculture: Nutrition, Bacteriostasis and Immunoregulation. *J. Appl. Microbiol.* 128, 28–40. doi: 10.1111/jam.14383

Wang, G. X., Li, F.-Y., Cui, J., Wang, Y., Liu, T.-Y., Han, J., et al. (2011). Immunostimulatory Activities of a Decapeptide Derived From *Alcaligenes Faecalis* FY-3 to Crucian Carp. *Scan. J. Immunol.* 74 (1), 14–22. doi: 10.1111/j.1365-3083.2011.02533.x

Wang, C. A., Liu, H. B., Mu, G. Q., Lu, S. X., Wang, D., Jiang, H. B., et al. (2019b). Effects of Traditional Chinese Medicines on Immunity and Culturable Gut Microflora to *Oncorhynchus Masou*. *Fish Shellfish Immunol.* 93, 322–327. doi: 10.1016/j.fsi.2019.07.071

Wang, Y., Wu, Y., Wang, Y., Xu, H., Mei, X., Yu, D., et al. (2017). Antioxidant Properties of Probiotic Bacteria. *Nutrients* 9, 521. doi: 10.3390/nu9050521

Wang, M., Yi, M., Lu, M., Gao, F., Liu, Z., Huang, Q., et al. (2020a). Effects of Probiotics *Bacillus Cereus* NY5 and *Alcaligenes Faecalis* Y311) Used as Water Additives on the Microbiota and Immune Enzyme Activities in Three Mucosal Tissues in Nile Tilapia *Oreochromis Niloticus* Reared in Outdoor Tanks. *Aquacult. Rep.* 17, 9. doi: 10.1016/j.aqrep.2020.100309

Wang, P., Zhou, Q. C., Feng, J., He, J. J., Lou, Y. D., and Zhu, J. Q. (2019c). Effect of Dietary Fermented Soybean Meal on Growth, Intestinal Morphology and Microbiota in Juvenile Large Yellow Croaker, *Larimichthys Crocea*. *Aquacult. Res.* 50 (3), 748–757. doi: 10.1111/are.13929

Wanka, K. M., Damerau, T., Costas, B., Krueger, A., Schulz, C., and Wuertz, S. (2018). Isolation and Characterization of Native Probiotics for Fish Farming. *BMC Microbiol.* 18, 119. doi: 10.1186/s2866-018-1260-2

Wu, S., Wang, G., Angert, E. R., Wang, W., Li, W., and Zou, H. (2012). Composition, Diversity, and Origin of the Bacterial Community in Grass Carp Intestine. *PLoSOne* 7 (2), e30440. doi: 10.1371/journal.pone.0030440

Wu, Z.-Q., Jiang, C., Ling, F., and Wang, G.-X. (2015). Effects of Dietary Supplementation of Intestinal Autochthonous Bacteria on the Innate Immunity and Disease Resistance of Grass Carp (Ctenopharyngodon Idellus). *Aquaculture* 438, 105–114. doi: 10.1016/j.aquaculture.2014.12.041

Yao, Y.-Y., Yang, Y.-L., Gao, C.-C., Zhang, F.-L., Xia, R., Li, G., et al. (2020). Surface Display System for Probiotics and its Application in Aquaculture. *Rev. Aquacult* 12 (4), 2333–2350. doi: 10.1111/raq.12437

Yi, C.-C., Liu, C.-H., Chuang, K.-P., Chang, Y. T., and Hu, S.-Y. (2019). A Potential Probiotic *Chromobacterium Aquaticum* With Bacteriocin-Like Activity Enhances the Expression of Indicator Genes Associated With Nutrient Metabolism, Growth Performance and Innate Immunity Against Pathogen Infections in Zebrafish (*Danio Rerio*). *Fish Shellfish Immunol.* 93, 124–134. doi: 10.1016/j.fsi.2019.07.042

Zhang, B., Li, C., Wang, X., Liu, C., Zhou, H., Mai, K., et al. (2020). Administration of Commensal *Shewanella* Sp. MR-7 Ameliorates Lipopolysaccharide-Induced

Intestine Dysfunction in Turbot (*Scophthalmus Maximus* L.). *Fish Shellfish Immunol.* 102, 460–468. doi: 10.1016/j.fsi.2020.04.068

Zhang, X., Shu, M. A., Wang, Y. B., Fu, L. Q., Li, W. F., Deng, B., et al. (2014). Effect of Photosynthetic Bacteria on Water Quality and Microbiota in Grass Carp Culture. *World J. Microbiol. Biotechnol.* 30 (9), 2523–2531. doi: 10.1007/s11274-014-1677-1

Zhan, P. R., and Liu, W. (2013). Use of Fluidized Bed Biofilter and Immobilized *Rhodopseudomonas Palustris* for Ammonia Removal and Fish Health Maintenance in a Recirculation Aquaculture System. *Aquacult. Res.* 44 (3), 327–334. doi: 10.1111/j.1365-2109.2011.03038.x

Zhou, X. X., Tian, Z. Q., Wang, Y. B., and Li, W. F. (2010). Effect of Treatment With Probiotics as Water Additives on Tilapia (*Oreochromis Niloticus*) Growth Performance and Immune Response. *Fish Physiol. Biochem.* 36 (3), 501–509. doi: 10.1007/s10695-009-9320-z

Zhou, S., Zhang, A., Yin, H. P., and Chu, W. H. (2016). *Bacillus* Sp. QSI-1 Modulate Quorum Sensing Signals Reduce *Aeromonas Hydrophila* Level and Alter Gut Microbial Community Structure in Fish. *Front. Cell. Infect. Microbiol.* 6. doi: 10.3389/fcimb.2016.00184

Ziólkowska, M., Rokicki, J., and Kedzia, A. (2009). The Effect of Infection by *Pomphorhynchus Laevis* (Acanthocephala) on the Composition of the Intestinal Bacterial Flora in Flounder, *Platichthys Flesus*. *J. Mar. Bio. Ass. United Kingdom* 89 (6), 1177–1179. doi: 10.1017/S0025315409000447

Zorriehzahra, M. J., Delshad, S. T., Adel, M., Tiwari, R., Karthik, K., Dhama, K., et al. (2016). Probiotics as Beneficial Microbes in Aquaculture: An Update on Their Multiple Modes of Action: A Review. *Vet. Quart.* 16 (4), 228–241. doi: 10.1080/16522176.2016.1172132

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.