Review article

Probiotics in shellfish aquaculture

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ARTICLE INFO	ABSTRACT

The shellfish aquaculture industry has dramatically developed during the last two decades. However, this development has, in some cases, resulted in environmental degradation, emergence of diseases and low productivity. The need for improving disease resistance, growth performance, feed efficiency, and safe aquatic production for human consumption has stimulated development and applications of probiotics in aquaculture. Probiotics used in shellfish aquaculture include genera of *Lactobacillus*, *Enterococcus*, *Bacillus*, *Aeromonas*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Clostridium*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodosporidium*, *Roseobacter*, *Streptomyces* and *Vibrio*. The beneficial effects of these probiotics include improved growth performance, enzymatic contribution to nutrition, inhibition of adherence and colonization of pathogenic bacteria in the digestive tract, modulation of the gut microbiota, and increase haematological parameters and immune response.

The present review addressed insight into the application of probiotics in shellfish aquaculture, methods of administration, mode of actions, and their enhancing effects, and discuss research gaps and issues that merit further investigations.

1. Introduction

In the 1970s and 1980s antibiotics were commonly used in disease control. However, the indiscriminate use of antibiotics used to treat infectious diseases led to selective pressure of antibiotic resistance, a property that may be transferred to other bacteria (Cabello, 2006; Romero, Feijoó, & Navarrete, 2012). Moreover, it is generally accepted that antibiotics administration in finfish and shellfish modulate the gut microbiota (Ringø et al., 2016), which in turn exerts negative effects on humans (Greenless, 2013; Salyers, Gupta, & Wang, 2014). Based on this fact, the European Union in 2003 banned the use of antibiotics in production. The use of probiotics is one of the alternative approaches to immunoprophylactic control in aquaculture, and is considered as a supplementary strategy or alternative to vaccines and chemicals.

There is a long history of health claiming microorganisms. According to Bottazzi (1983), the Roman historian Plinius in 76 B.C. recommended administration of fermented milk products for treating gastroenteritis. The word *probiotic* stems from the Greek roots *pro* and *bios*, or *"profile"* (Schrezenmeir & de Vrese, 2001), and several definitions of probiotics have been put forward since the first definition was given by Lilly and Stillwell (1965), but the most widely used is the definition by World Health Organisation's (WHO); *"live microorganisms that when administrated in adequate amounts, confer a health benefit to the host"*. During the last decades, several reviews have addressed on probiotics and their impacts in shellfish aquaculture as growth promoters, nutritional, environmental capacity, as immunostimulants and advantage as prophylactic against infectious diseases (Ayisi, Apraku, & Afriyie, 2017; Cordero, Esteban, & Cuesta, 2014; Farzanfar, 2006; Hoseinifar, Dadar, van Doan, & Harikrishnan, 2019; Hoseinifar, Sun, Wang, & Zhou, 2018; Kuebutornye, Abarike, & Lu, 2019; Kumar, Roy, Meena, & Sarkar, 2016; Li et al., 2018; Ninawe & Selvin, 2009; Shefat, 2018; Soltani et al., 2019; van Hai et al., 2009a; van Hai and Fotedar, 2010).

Even though information was presented in the above mention reviews, the present review address to present an update on probiotics in shellfish aquaculture, and on probiotics data not mention in the aforementioned reviews. In order to avoid overlaps, studies discussed in the aforementioned reviews are only briefly presented in the text and Tables.

In shellfish aquaculture, several probiotics species are used; *Lactobacillus*, *Enterococcus*, *Bacillus*, *Aeromonas*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Clostridium*, *Microbacterium*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodosporidium*, *Roseobacter*, *Streptomyces* and *Vibrio*. To my knowledge, the first studies on the use of probiotics in shellfish aquaculture was carried out by Maeda and Liao (1992, pp. 25–29) and Nogami and Maeda (1992), using bacterial strain PM-4 originally isolated from a crustacean culture pond, but since then numerous studies have been carried out (Table 1 –

Table 1
Effect of lactic acid bacteria (LAB) on growth performance, immune response and disease resistance in shrimp culture.

Species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
LAB	Shrimp gut	1.5×10^8 CFU mL^{-1}/60 days	Pacific white shrimp (Litopenaeus vannamei)	↑ Survival, resistance against V. harveyi	Vieira et al. (2007) [a]
LAB strains	National Collection, Pune, India	5×10^6 cells g^{-1}/ 4 weeks	Penaeus indicus	↑ Resistance against V. parahaemolyticus	Ajitha et al. (2004) [b]
LAB strain NS61	Giant lion's paw scallop	10^4 CFU mL^{-1}/ 11 days	Cortez oyster (Crassostrea corteziensis) larvae	↑ Survival → Growth	Campa-Cordova et al. (2011)
Enterococcus					
E. faecium	National Collection, Pune, India	5×10^6 cells g^{-1}/ 4 weeks	Pacific white shrimp	↑ Resistance against V. parahaemolyticus	Ajiha et al. (2004) [b]
E. faecium	N/A	10^7 CFU g^{-1}/ N/A about duration	Giant tiger prawn (P. monodon)	↑ Resistance against V. harveyi and V. parahaemolyticus	Swain et al. (2009) [b]
E. faecium	N/A	10^6 CFU g^{-1}/ 4 weeks	Pacific white shrimp	↑ Survival, adhesive activity, expression of immune and digestion related genes in the mid gut	Sha et al. (2016a, 2016b)
E. faecium	Shrimp intestine	N/A	Giant tiger prawn	↑ Growth and resistance against Vibrio	Shefat (2018)
Lactococcus					
Lac. garvieae	N/A	10^7 CFU g^{-1}/ N/A about duration	Giant tiger prawn	↑ Resistance against V. harveyi	Swain et al. (2009) [b]
Lac. lactis	Shrimp intestine	10^5 CFU g^{-1}/7 days	M. japonicus	↑ Up regulation of lysozyme gene expression in intestine and hepatopancreas, and resistance against V. penaeicida → anti-lipopolysaccharide factor, superoxide dismutase, prophenoloxidase and toll-like receptor	Maeda et al. (2014)
Lac. lactis	Pacific white shrimp intestine	$2\text{-}4 \times 10^8$ cells g^{-1}/ 16 days	Pacific white shrimp	↑ Haemolymph PO activity, relative mRNA expression of LvproPO1, LvproPO2 and resistance against V. parahaemolyticus	Chomwong et al. (2018)
Lac. lactis subsp. lactis	Intestine of Pacific white shrimp	10^6, 10^7, and 10^8 CFU g^{-1}/ 8 weeks	Pacific white shrimp	↑ Growth performance, digestive enzymes activities, Lactobacillus and Bacillus counts, Vibrio counts and resistance against V. anguillarum	Adel et al. (2017a) [d]
Lactobacillus					
Lactobacillus sp.	Digestive tract of chicken	$\sim 10^{10}$ CFU g^{-1}/ 100 days	Giant tiger prawn	↑ Growth, survival and resistance against V. harveyi	Phianphak et al. (1999) [c]
Lactobacillus sp. AMET1506	Curd	10^6 CFU g^{-1}/30 days	Pacific white shrimp	↑ Resistance against V. harveyi	Karthik et al. (2014)
Lactobacillus sp. AMET1506	Curd	10^5 CFU g^{-1}/30 days	Pacific white shrimp	↑ Total heterotrophic bacterial load and LAB counts in intestine Reduced the bacterial load of E. coli, Salmonella spp. and Shigella spp. in intestine	Karthik et al. (2015)
Lactobacillus sp.	Intestine of Pacific white shrimp	10^7 CFU g^{-1}/27 days	Pacific white shrimp	↑ Body weight, digestive enzyme activities and resistance against WSSV	Zuo et al. (2019) [d]
Lb. acidophilus	Homemade curd	10^5 CFU g^{-1}/30 days	Giant tiger prawn	↑ Resistance against V. alginolyticus	Sivakumar et al. (2012) [b]
Lb. acidophilus	Homemade curd	10^6 cells g^{-1}/ one month	Macrobrachium rosenbergii	↑ Growth and resistance against Vibrio spp.	Khan and Mahmud (2015)
Lb. brevis MTCC 4463	Culture collection	Dose N/A/90 days	M. rosenbergii	↑ Growth performance, digestive enzymes and body composition Probiotic administration modulate the gut microbiota	Karthik and Bhavan (2018)
Lb. bulgaricus	National Collection, Pune, India	5×10^6 cells g^{-1}/ 4 weeks	Penaeus indicus	↑ Resistance against V. parahaemolyticus	Ajitha et al. (2004) [b]
Lb. bulgaricus	Intestine of Pacific white shrimp	10^7 and 10^9 CFU g^{-1}/30 days	Pacific white shrimp	↑ Immune response and disease resistance	Roomiani et al. (2018) [d]
Lb. pentosus	N/A	10^6 CFU g^{-1}/ 4 weeks	Pacific white shrimp	↑ Survival, adhesive activity, expression of PEN-3α, proPO, trypsin and α-amylase in the mid gut, and proPO, LGBP, IveLee, trypsin and α-amylase in the hepatopancreas	Sha et al. (2016a) [b]

Table 1 (*continued*)

Species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Lb. pentosus	Intestine of healthy *Acanthogobius hasta*	10^7 CFU g^{-1}/ 4 weeks	Pacific white shrimp	↑ Abundance of intestinal Actinobacteria → improvements of intestinal histology	Sha et al. (2016c) [b]
Lb. pentosus	Intestinal tract of abalone	10^3, 10^5, and 10^7 CFU g^{-1}/8 weeks	*Haliotis discus hannai*	↑ SR, Food intake, shell length-specific growth rate, FCR, antioxidant capacity and resistance against *V. parahaemolyticus*	Gao et al. (2018) [d]
Lb. pentosus	Gut of Branded goby (*Chaeturichthys stigmatias*)	5×10^8 CFU g feed^{-1}/ 4 weeks	Pacific white shrimp	↑ Digestion related enzymes, resistance against *V. parahaemolyticus* and induced stress response genes expression	Du et al. (2019) [d]
Lb. plantarum	Shrimp isolate	10^7 and 10^{10} CFU kg^{-1}/168 h	Pacific white shrimp	↑ immune response, gut microbiota, resistance against *V. alginolyticus*	Chiu, Guu, Liu, Pan, and Cheng (2007) [a]
Lb. plantarum	Pacific white shrimp	2×10^{10} CFU kg^{-1}/8 days	Pacific white shrimp	→ Total bacterial and LAB counts in the digestive tract Reduced *Vibrio* counts in the digestive tract	Vieira et al. (2008)
Lb. plantarum	Broodstock shrimp	1.5×10^8 CFU g^{-1}/ 60 days	Pacific white shrimp	↑ Total LAB counts and resistance against *V. harveyi* Decreased total bacterial counts and total *Vibrio* counts	Vieira et al. (2010)
Lb. plantarum	N/A	3.16×10^9 CFU g^{-1}/60 days	Giant freshwater prawn (*M. rosenbergii*)	↑ Specific growth rate, weight gain and phenoloxidase → Survival, total haemocyte counts and respiratory burst	Rahiman et al. (2010)
Lb. plantarum	Commercial	3.3×10^{11} CFU g^{-1} feed; 0, 0.001, 0.01, 0.1 and 1 g/30 days	Pacific white shrimp	↑ Growth performance and stress resistance at 1 g inclusion ↑ Survival at 0.1 g inclusion → protease activity	Tung et al. (2010)
Lb. plantarum	Pacific white shrimp	2–4×10^8 CFU g^{-1} feed/42 days	Pacific white shrimp	↑ Disease resistance against *V. harveyi*	Kongnum and Hongpattarakere (2012)
Lb. plantarum	Gut of female blue swimming crab	10^6, 5×10^6, and 10^7 CFU mL^{-1}/14 days	*Portunus pelagicus*	↑ Survival, protease – and amylase activities, total bacterial- and *Vibrio* counts in tank water → Nitrogen content and pH of culture water	Talpur et al. (2013)
Lb. plantarum	Culture collection	10^7, 10^8, and 10^9 CFU g^{-1} diet/ 90 days	*Macrobrachium rosenbergii*	↑ WG, SGR, FCE, PER, FCR, carcass protein content, LAB counts in intestine, total hemocyte count, phenol oxidase- and respiratory burst activities and resistance against *A. hydrophila* ↓LAB counts after switching back to basal diet	Dash et al. (2014) [d]
Lb. plantarum	Culture collection	10^7, 10^8, and 10^9 CFU L^{-1} diet/ 90 days	*M. rosenbergii*	↑ WG, SGR, FCE, PER, FCR, carcass protein content → Water quality	Dash et al. (2016) [d]
Lb. plantarum	Pacific white shrimp intestine	10^7 mL^{-1}/4 weeks	Pacific white shrimp	↑ Phenoloxidase activity, intestinal LAB and resistance against *V. alginolyticus* → Growth performance, total heterotrophic bacteria in intestine and intestinal *Vibrio* counts	Ramirez et al. (2017)
Lb. plantarum	Commercial probiotic	10^9 CFU mL^{-1}/ 45 days	Pacific white shrimp	↑ Final weight, WG, SGR, FCR and improved the resistance against the stress of acute low salinity	Zheng et al. (2017) [d]
Lb. plantarum	Pacific white shrimp intestine	2–4×10^8 cells·g^{-1}/ 16 days	Pacific white shrimp	↑ Haemolymph PO activity, relative mRNA expression of *LvproPO1*, *LvproPO2* and resistance against *V. parahaemolyticus*	Chomwong et al. (2018)
Lb. plantarum	Shrimp intestine	1.0×10^7 CFU mL^{-1}/ 35 days	Pacific white shrimp	→ Growth performance and water quality	Correa et al. (2018) [d]
Lb. plantarum T8	Hepatopancreas from Pacific white shrimp	N/A/10 weeks + 2 days challenge	Pacific white shrimp	↑ Growth and resistance against *V. parahaemolyticus*	Nguyen et al. (2018)
Lb. plantarum T13	Hepatopancreas from Pacific white shrimp	N/A/10 weeks + 2 days challenge	Pacific white shrimp	↑ Resistance against *V. parahaemolyticus* → Growth	Nguyen et al. (2018)
Lb. plantarum	Commercial probiotic	20×10^3 cells mL^{-1} and 1×10^8 (CFU) mL^{-1}/45 days	Pacific white shrimp	↑ Improve water quality in biofloc system Reduce shrimp diseases and environmental impact	Pacheco-Vega et al. (2018) [d]
Lb. plantarum	Wild shrimp intestine	N/A	Pacific white shrimp	↑ Resistance against *V. harveyi*	Shefat (2018)
Lb. plantarum	Shrimp intestine	N/A	Pacific white shrimp	↑ Resistance against *Vibrio*	Shefat (2018)

Table 1 (*continued*)

Species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Lb. plantarum	Commercial probiotic	10^9 CFU mL^{-1}/15 days	Pacific white shrimp	↑ Final weight, WG, SGR, FCR, digestive enzyme activities and enterocytes height	Zheng et al. (2018) [d]
Lb. plantarum	Intestine of rainbow trout	0, 10^7 (LB7), 10^8 (LB8), and 10^9 (LB9) CFU g^{-1} diet/97 days	Crayfish (*Astacus leptodactylus*)	↑ Total haemocyte count, semi granular cells, hyaline cells count, total plasma protein and phenoloxidase by LB7 and LB8 administrations; ↑ Superoxide dismutase and catalase by LB7 administration; ↑ Protease-, amylase- and alkaline phosphatase by LB8 and LB9 administration; → Autochthonous intestinal bacteria counts	Valipour et al. (2019)
Lb. sporogenes	Commercial probiotic	0%, 1%, 2%, 3% and 4%/90 days	*M. rosenbergii*	↑ SR, WG, SGR, FCE and PER, FCR, total protein, total free amino acid, total carbohydrate, and total lipid content, feeding rate, absorption rate, conversion rate and excretory rate	Seenivasan et al. (2014) [d]
Pediococcus					
P. acidilactici	Commercial probiotic	10^7 CFU g^{-1} feed/1 month	Litopenaeus stylirostris	↑ Antioxidant status, resistance against V. nigripulchritudo	Castex et al. (2010) [b]
P. pentosaceus	Intestine of Pacific white shrimp	0, 10^6, 10^7, and 10^8 CFU g^{-1} diet/8 weeks	Pacific white shrimp	↑ Final weight, final length, WG, SR, WG, FCR, protease and amylase activities, *Lactobacillus* sp. and *Bacillus* sp. intestinal counts	Adel, Yeganeh, Dawood, Safari, and Radhakrishnan (2017b) [d]
Streptococcus					
S. cremoris	National Collection, Pune, India	5×10^6 cells g^{-1}/4 weeks	Penaeus indicus	↑ Resistance against V. parahaemolyticus	Ajitha et al. (2004) [b]
S. phocae	Intestine of P. indicus	Dose N/A/15 days	Giant tiger prawn	↑ Resistance against V. harveyi	Kanmani et al. (2010)
S. phocae	N/A	10^7 CFU g^{-1}/N/A about duration	Giant tiger prawn	↑ Specific growth rate and resistance against V. harveyi	Swain et al. (2009)
S. phocae	Commercial	10^8 CFU mL^{-1}/30 days	Giant tiger prawn	↑ Total hemocyte counts, phenol oxidase-, phagocyte activities, respiratory burst and resistance against V. parahaemolyticus	Pattukumar et al. (2013)
S. phocae	Fish intestine	N/A	Giant tiger prawn	↑ Resistance against Vibrio	Shefat (2018)
Mixture of LAB					
Lb. acidophilus, Lb. bulgaricus, Lb. casei, Lb. casei subsp. *tolerans* and *Lb. jensenii*	GI tract of chicken	10^{10} CFU g^{-1}/100 days	Giant tiger prawn	↑ Growth and resistance against V. harveyi	Phianphak et al. (1999)
Lb. plantarum, Lb. salivarius and *Lb. rhamnosus*	Gut of female P. pelagicus	10^6, 5×10^6 and 10^7 CFU mL^{-1}/14 days	P. pelagicus	↑ Growth and digestive enzyme (protease and amylase) activities by multiple probiotics	Talpur et al. (2012)
PrimaLac© (*Lb. acidophilus, Lb. casei, E. faecium* and *B. bifidium*)	N/A	0.25, 0,5 and 10 g kg^{-1}/60 days	Pacific white shrimp	↑ Weight gain, specific growth rate, body, body crude protein, FCR, protease, amylase, lipase and penaeidin gene expression; ↓ body crude lipid and body moisture	Miandare et al. (2016)
E. faecium and *Lb. pentosus*	Gut of Fenneropenaeus chinensis) and Chaeturichthys stigmatias	1×10^7 CFU^{-1} g feed/4 weeks	Pacific white shrimp	↑ Resistance against V. parahaemolyticus	Sha et al. (2016b) [d]
E. faecalis and *E. faecium*	Intestine of prawn and mullet	Dose N/A/ Duration N/A	Pacific white shrimp	↑ Resistance against A. hydrophila and V. vulnificus	Cui et al. (2017)
S. faecium, S. thermophilus, Lb. acidophilus, Lb. bulgaricus, Lb. johnsonii, Lb. plantarum, B. bifidium, Aspergillus ourozai and *Candida pentolopsy*	Commercial	2×10^9 CFU g^{-1}/28 days	Pacific white shrimp	↑ Growth performance; → Counts of coliforms and S. aureus; ↓ Total bacterial counts and C. perfringens	Javadi and Khatibi (2017)
Combination of LAB and Bacillus					

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Table 1 (continued)

Species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Enterococcus sp., Lactobacillus sp. and Bacillus sp.	N/A	6×10^3 CFU mL^{-1}/30 days	Pink shrimp (Farfantepenaeus brasiliensis)	↑ Final weight, specific growth rate; Higher levels of total protein and granular haemocyte; Lower Vibrio counts in water	de Souza et al. (2012)
Molasses and Lactobacillus and Bacillus	N/A	253.5 kg pond^{-1}/2.2 $\times$ 10^8 CFU g^{-1}/16 weeks	Pacific white shrimp	→ Dissolved O$_2$, temperature, salinity, total heterotrophic bacteria, FCR, final weight and survival	Maia, Modesto, Brito, Galvez, and Gesteira (2016)
Lactobacillus and Bacillus	N/A	2.2×10^8 CFU g^{-1}/16 weeks	Pacific white shrimp	↑ Total heterotrophic bacteria count in the sediment, concentration of Pyrrophyta algae, and in water and sediment quality	De Paiva-Maia et al. (2013)
Lactobacillus, B. subtilis and B. licheniformis	N/A	3×10^7 CFU kg^{-1}, 1.8×10^8 CFU kg^{-1} and 2×10^7 CFU kg^{-1}/8 weeks	Pacific white shrimp	↑ Growth performance, superoxide dismutase, catalase, alkaline phosphatase, lysozyme, lipase and amylase activities, intestinal villi heights and microbial gut diversity	Xie et al. (2019)

N/A: no information available.
Genera abbreviations: E. – Enterococcus; Lac. – Lactococcus; Lb. – Lactobacillus; P. – Pediococcus; Str. – Streptococcus; W. – Weissella; V. – Vibrio.
↑ - positive effect; ↓ - negative effect; → - no effect.
[a] Studies discussed in the review of Ninawe and Selvin (2009).
[b] Studies discussed in the review of Hoseinifar et al. (2018).
[c] Studies discussed in the review of Kumar et al. (2016).
[d] Studies discussed in the review of Ringø, van Doan, Lee, & Song (2019).

3).

Shellfish aquaculture plays an important role in the world economy, and according to FAO (2016) brackish and marine shrimp production have increased from less than 10.000 metric tonnes in 1970 to more than 4.000.000 metric tonnes in 2014, and most of the aquaculture shrimp production come from Pacific white shrimp (*Litopenaeus vannamei*) which accounts for 80% of the production. However, as pathogenic bacteria cause enormous economic loss, an alternative to chemotherapies and antibiotics is probiotics. The present review highlight probiotics as a key factor in sustainable shellfish aquaculture, and present information on the use of probiotics by their stimulating effect on growth performance, innate immune response and improved resistance towards pathogenic microbial infection.

2. Methods of probiotic administration

To my knowledge, the first application of probiotics in aquaculture was carried out by Kozasa (1986), but since then the environment-friendly treatment has increased rapidly, and several comprehensive aquaculture reviews have been published (e.g. Gatesoupe, 1999; Hoseinifar et al., 2018; Ringø et al., 2014; Ringø et al., 2018; van Hai, Buller, & Fotedar, 2010; Verschuere, Rombaut, Sorgeloos, & Verstraete, 2000). With regard to the use of probiotics, it is essential to investigate the best way of administration, optimal dose, and the technical solutions required; especially to keep the probiotics alive in dry pellets (Gatesoupe, 1999).

Probiotic administrations mainly depends on several factors i.e. the probionts, supplementation form, vector of administration, dosage level and duration of application, and several different administration modes have been used:

i) Oral administration via diet or water/bath. Supplementation to the diet is the most widely used administration method. Generally, probiotics and cell wall components (parabiotics) are applied in the feed, added to the entire tank or pond water to confer protection against infection (Verschuere et al., 2000). In fish- and shellfish larvae, live food (e.g. *Artemia*) has proved to be an efficient carrier of probiotics (e.g. Giarma, Amanetidou, Toufexi, & Touraki, 2017; van Hai et al., 2010).

ii) Administration of several probiotics in combination. In his pioneer review devoted to "Probiotics in man and animals," Fuller (1989) wrote, "Probiotic preparations may consist of single strains or may contain any number up to eight strains." However, since the early 1990s most probiotic studies in aquaculture used single administration, but during the last decade, supplementation of multiple probiotics in the diets to aquatic animals has gained interest (e.g. Mohapatra et al., 2014; Allameh et al., 2016; Zorriehzahra et al., 2016; Kesselring, Gruber, Standen, & Wein, 2019; Mukherjee, Chandra & Ghosh, 2019). The advantage of multiple-strain preparations is; they are active against wider range of conditions and species.

iii) Inactivated bacteria. For example, oral administration of heat-inactivated *Lactobacillus delbrueckii* ssp. *lactis* and *Bacillus subtilis*, individually or combined (Salinas et al., 2008).

iv) Spores, a structure produced by few bacteria genera is resistant to many environmental or induced factors that the bacteria may be subjected to. The spores help the bacteria to survive by being resistant to extreme changes in the bacteria's habitat including extreme temperatures, lack of moisture/drought, or being exposed to chemicals and radiation. Bacterial spores can also survive at low nutrient levels, and according to Elisashvili, Kachlishvili, and Chikindas (2019) spore-forming probiotic bacteria have received increased scientific and commercial interest. Several studies listed in Table 2, have used bacilli spores.

v) Culturing, storing and administration. Probiotics are usually added to feed as freeze-dried cultures, which are sometimes mixed with

Table 2
Effect of *Bacillus* on growth performance, immune response and disease resistance in shrimp culture.

Bacillus species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Bacillus sp. S11	Intestine of giant tiger shrimp	~10^{10} CFU g^{-1} feed/100 days	Giant tiger shrimp (*P. monodon*)	↑ MSW, disease resistance against *Vibrio harveyi*	Rengpipat et al. (1998a, b) [a]
Bacillus sp. S11	Intestine of giant tiger shrimp	~10^{10} CFU g^{-1} feed/90 days	Giant tiger shrimp	↑ MSW, phagocytosis, phenoloxidase, disease resistance against *V. harveyi*	Rengpipat et al. (2000) [a]
Bacillus sp. S11	Intestine of giant tiger shrimp	~10^{10} CFU g^{-1}/100 days	Giant tiger shrimp	↑ ARG, disease resistance against *V. harveyi*	Rengpipat et al. (2003) [a]
Bacillus sp. S11	Intestine of giant tiger shrimp	~10^{10} CFU g^{-1}/90 days	Pacific white shrimp (*L. vannamei*)	↑ Survival, total haemocyte, granular haemocyte counts, phenoloxidase and disease resistance against *Vibrio harveyi*	Sapcharoen and Rengpipat (2013)
Bacillus sp.	Sediment	10^{11}/0.8 ha pond	Giant tiger shrimp	↑ ARG, disease resistance against *Vibrio* sp.	Dalmin et al. (2001) [a]
Bacillus OJ	Intestine of Pacific white shrimp	10^8 and 10^{10} CFU g^{-1}/28 days	Pacific white shrimp	↑ Phenoloxidase, phagocytosis, respiratory burst, acid phosphatase, resistance against white spot disease	Li et al. (2009) [a]
Bacillus NL110	N/A	$4.73 \pm 2.87 \times 10^9$ CFU g^{-1a}/twice a day for 60 days	Giant freshwater prawn (*M. rosenbergii*)	↑ SGR, WG, survival, ARG, total hemocyte count, phenoloxidase activity, respiratory burst	Rahiman et al. (2010)
Bacillus PC465	Intestine of Chinese white shrimp (*F. chinensis*)	10^8 and 10^9 CFU g^{-1}/30 days	Pacific white shrimp	↑ Growth rate, amylase, protease, histology, transcription of penaeidin 3a, peroxinectin, C-type lectin 3, and thioredoxin in hemocytes, and disease resistance against white spot syndrome virus	Chai et al. (2016)
Bacillus MJA1.1	Mucus of tilapia (*Oreochromis* sp.)	Dose N/A/30 days	Giant tiger shrimp	↑ Survival and survival and resistance of shrimp exposed to ammonia stress → Growth	Doroteo, Pedroso, Lopez, and Apines-Amar (2018)
B. aquimaris	Intestine of shrimp*	> 3×10^6 CFU g^{-1}/4 weeks	Pacific white shrimp	↑ Growth and phenoloxidase activity	Ngo et al. (2016)
B. aryabhattai	Sediment from shrimp farm	10^8 CFU g^{-1}/6 weeks	Pacific white shrimp	Upregulation of antioxidant enzymes (C-type lec, pen3a, hsp60, trx and fer) ↑ Phenoloxidase, total antioxidant activity and disease resistance against *V. harveyi* → Total hemocyte count and superoxide dismutase in plasma and hepatopancreas	Tepaamorndech et al. (2019) [a]
B. cereus biovar toyoi	N/A	10^5 CFU mL^{-1}/duration N/A	Giant tiger shrimp	↓ Survival	Guo et al. (2009)
B. cereus	Giant tiger shrimp	0.1–0.4% per 100 feed/90 days	Giant tiger shrimp	↑ SGR, FCE, AGR, FCR, phenoloxidase, lysozyme, respiratory burst, bactericidal activity and disease resistance against *V. harveyi*	Chandran et al. (2014) [a]
B. cereus	Intestine of mud crab	Not tested in an *in vivo* experiment	Mud crab (*Scylla paramamosain*)	As the strain showed less probiotic characteristics compared to *B. pumilus* and *B. subtilis* it was not tested *in vivo*	Wu et al. (2014)
B. cereus	Pacific white shrimp	10^8 CFU g^{-1}/24 days	Pacific white shrimp	↑ Weight gain → Disease resistance against *V. parahaemolyticus*	Vidal et al. (2018)
B. cereus	Intestine of adult freshwater prawn (*M. rosenbergii*)	10^4 CFU g^{-1}/28 days	Giant freshwater prawn	↑ Growth, propionic acid level, superoxide dismutase → Acetic and butyric acid level, and disease resistance against *A. hydrophila*	Wee, Mok, Romano, Ebrahimi, and Natrah (2018)
B. coagulans	Intestine of common carp (*Cyprinus carpio*)	Three concen-trations of lyophilized *Rhodobacter sphaeroides* and *B. coagulans*/28 days	Pacific white shrimp	↑ Growth performance and digestive enzyme (protease, amylase and lipase) activities	Wang (2007)
B. coagulans	Pond sediment of shrimp	10^5, 5×10^5 and 10^6 CFU mL^{-1}/duration N/A	Pacific white shrimp	↑ Survival and digestive enzyme activities	Zhou et al. (2009)
B. coagulans	Culture collection	10^7 CFU g^{-1}/50 days	Pacific white shrimp	↑ Final weight, daily weight gain, survival rate, and protease-, amylase- and lipase activities → Muscle composition of moisture, crude protein and ash	Wang et al. (2012)
B. coagulans ATCC 7050	Culture collection	10^6–10^8 CFU g^{-1}/56 days	Pacific white shrimp	↑ Growth performance, immune- and antioxidant response, digestive enzyme activities and intestinal morphology	Amoah et al. (2019)
B. flexus	Pond water/sediment	10^5 CFU mL^{-1}/21 days	Pacific white shrimp	↑ Growth performance, innate immune enzyme- and digestive enzyme activities, stress tolerance and disease resistance against *V. harveyi* → Total bacterial counts in water ↓ *Vibrio* counts in water	Cai et al. (2019)

Table 2 (*continued*)

Bacillus species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
B. fusiformis	N/A	10^5 CFU mL^-1/duration N/A	Pacific white shrimp	↑ Survival	Guo et al. (2009)
B. licheniformis	Surface sediment of shrimp pond	10^3, 10^4 and 10^5 CFU mL^-1/40 days	Pacific white shrimp	↑ Haemocyte counts, phenoloxidase and superoxide dismutase activities; → Total bacterial counts in the intestinal tract; ↓ Vibrio numbers in the intestinal tract	Li et al. (2007)
B. licheniformis	Pond water/sediment	10^5 CFU mL^-1/21 days	Pacific white shrimp	↑ Growth performance, innate immune enzyme- and digestive enzyme activities, stress tolerance and disease resistance against V. harveyi; → Total bacterial counts in water; ↓ Vibrio counts in water	Cai et al. (2019)
B. megaterium	N/A	1.2 × 10^4 CFU kg^-1 feed/4 weeks	Pacific white shrimp	↑ Stress tolerance; → Growth performance and haemolymph metabolites	Olmos, Ochoa, Paniagua-Michel, and Rosalia (2011)
B. pumilus	Marine environment	10^6 CFU mL^-1/18 days	Giant tiger shrimp	↑ total ammonia and nitrite; → pH, salinity, dissolved oxygen and temperature	Banerjee et al. (2010)
B. pumilus	Intestine of mud crab	10^5 CFU g^-1/30 days	Mud crab (Scylla paramamosain)	↑ Expression of immune related genes (catalase, prophenoloxidase and superoxide dismutase), respiratory burst activity and disease resistance against V. parahaemolyticus	Wu et al. (2014)
B. pumilus	Commercial	10^6, 10^7 and 10^8 CFU g^-1 feed/60 days	Giant freshwater prawn	↑ Weight gain rate, specific growth rate, phagocytic-, respiratory burst-, and catalase activities, nitric oxide synthase and acid phosphatase activities, phenoloxidase-, amylase- and protease activities	Zhao et al. (2019)
B. stratosphericus	N/A	4–5 x 10^10 CFU g^-1/180 days	Abalone (Haliotis diversicolor)	↑ Shell length, wet weight, glutathione peroxidase-, catalase-, alkaline phosphatase-, acid phosphatase- and superoxide dismutase activities; → Disease resistance against V. harveyi; Modulate gut microbiota	Zhao et al. (2018)
B. subtilis BT23	Shrimp culture pond	10^6–10^8 CFU mL^-1/6 days	Giant tiger shrimp	↑ Disease resistance against V. harveyi	Vaseeharan and Ramasamy (2003) [a]
B. subtilis	Intestine of adult Pacific white shrimp	10^5 CFU g^-1/28 days	Pacific white shrimp	↑ Survival, final weight, feed conversion ratio and disease resistance against V. parahaemolyticus	Balcázar et al. (2007)
B. subtilis E20	Fermented soybeans	10^6–10^8 CFU kg^-1 feed/7 days	Pacific white shrimp	↑ WG, FCR and survival	Liu, Chiu, Ho, and Wang (2009) [a]
B. subtilis E20	Fermented soybeans	10^6, 10^7 and 10^8 CFU kg^-1 feed/108 days	Pacific white shrimp	↑ Phenoloxidase, phagocytosis and disease resistance against V. alginolyticus	Tseng et al. (2009) [a]
B. subtilis E20	Fermented soybeans	10^8 and 10^9 CFU L^-1/14 days	Pacific white shrimp	↑ Larval survival (10^9 CFU L^-1), postlarvae survival (10^8 and 10^9 CFU L^-1) and in immune-related gene expression; → Total bacterial count and presumptive Vibrio count	Liu et al. (2010)
B. subtilis	N/A	1.2 × 10^4 CFU kg^-1 feed/4 weeks	Pacific white shrimp	↑ Growth performance, stress tolerance and haemolymph metabolites	Olmos et al. (2011) [a]
B. subtilis	Fermented pickles	10^5 and 10^8 CFU kg^-1 feed/8 weeks	Pacific white shrimp	↑ SGR, survival, digestive enzyme activities, up-regulated immune-related genes and disease resistance against V. harveyi; → FCR	Zokaeifar et al. (2012) [a]
B. subtilis	Juvenile freshwater prawn	10^8 CFU kg^-1 feed/60 days	Freshwater prawn (Macrobrachium rosenbergii)	↑ Growth, survival and disease resistance against A. hydrophila	Keysami and Mohammadpour (2013)
B. subtilis	Pacific white shrimp	5 × 10^9, 5 × 10^10 and 5 × 10^11 CFU kg^-1/8 weeks	Pacific white shrimp	↑ Phagocytic rate, lysozyme, superoxide dismutase phenoloxidase and antibacterial activity and disease resistance against V. harveyi; ↓ Body crude lipid	Liu et al. (2014)

Table 2 (*continued*)

Bacillus species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
B. subtilis	Intestine of mud crab	10^5 CFU g^{-1}/30 days	Mud crab	↑ Expression of immune related genes (catalase, prophenoloxidase and superoxide dismutase), respiratory burst activity and disease resistance against V. parahaemolyticus	Wu et al. (2014)
B. subtilis	Fermented pickles	10^5 and 10^8 CFU g^{-1}/8 weeks	Pacific white shrimp	↑ Growth (final weight and weight gain, activity of protease, amylase and disease resistance against V. harveyi	Zokaeifar et al. (2014) [a]
B. subtilis IPA-S.51	Hepatopancreas/stomach of Pacific white shrimp	10^6 CFU g^{-1}/45 days	Pacific white shrimp	↑ FW; Vibrio counts in intestine and faeces increased during probiotic administration.	Interaminense et al. (2018)
B. subtilis	N/A	10^9 CFU kg^{-1}/56 days	Pacific white shrimp	↑ Growth performance, apparent digestibility coefficient (ADC) of dry matter, crude protein and amino acids → ADC of crude lipid	Tsai, Chi, and Liu (2019)
B. thuringiensis	Pacific white shrimp	Dose N/A Duration N/A	Pacific white shrimp	↑ Disease resistance against V. anguillarum	Dou et al. (2016)
B. vireti	Intestine of freshwater prawn	10^8 CFU mL^{-1}/2 weeks	Freshwater prawn	↑ Antioxidant enzyme activities in muscle, hepatopancreas and gills, and disease resistance against P. aeruginosa	Hindu et al. (2018)
Mixture of Bacillus					
B. subtilis, B. subtilis, B. megaterium and B. thuringiensis	Intestine of Giant tiger prawn and shrimp pond	Live sprayed (LS), log 9.98 CFU mL^{-1}, freeze-dried (FD), 9.29 CFU g^{-1}/120 days	Giant tiger prawn	↑ Bacillus counts in hepatopancreas and intestine by LS and FD feeding → Culturable bacteria counts in hepatopancreas, intestine and cultured water ↓ Vibrio counts in hepatopancreas, intestine and cultured water by probiotic feeding; Modulate the bacterial community in hepatopancreas and intestine by LS and FD feeding	Boonthai et al. (2011)
Probiotic mixture A: B. thuringiensis, B. megaterium, B. polymyxa, B. licheniformis, B. subtilis, Debaryomyces hansenii and Rhodotorula; Probiotic mixture B: B. subtilis, B. polymyxa, B. megaterium, B. circulans and B. pumilus	Intestine of Pacific white shrimp	10^9 CFU mL^{-1}/duration N/A	Pacific white shrimp	↑ Growth performance, survival rate; number of beneficial microbial probiotics in shrimp larvae and postlarvae, and bacterial community in culture water	Nimrat et al. (2011)
B. subtilis and B. licheniformis	Commercial	0.5, 1, 2 and 3 g m^{-3}/9 weeks	Pacific white shrimp	→ Growth performance, water quality, total bacterial load and Vibrio counts in water and phytoplankton	Ferreira et al. (2017)
Three Bacillus strains	Tunisian hypersaline	10^6 CFU mL^{-1}/duration N/A	Pacific oyster (C. gigas)	↑ Resistance toward V. harveyi ↓ hemocytes mortality	Fdhila et al. (2017)
Bacillus and PHB					
Bacillus sp. JL47	Shrimp pond	4 g wet bacterial weight kg^{-1}/30 days	Giant tiger shrimp postlarvae	↑ Growth performance, survival, resistance against ammonia stress and resistance toward V. campbellii	Laranja et al. (2014)
Artemia larvae enriched with Bacillus sp. JL47	Shrimp pond	Enriched Artemia/15 days	Giant tiger shrimp postlarvae	↑ Relative expression of innate immune genes for ProPO, transglutaminase (Tgase) and heat shock protein 70 (Hsp70) after challenge with V. campbellii	Laranja et al. (2017)
Commercial Bacillus					
B. subtilis and B. licheniformis	Commercial	5×10^{10} CFU g^{-1}/45 days	Pacific white shrimp	↑ Total bacterial abundance ↓ Abundance of Vibrio	Hostins et al. (2017)
Bacillus and Gamma-proteobacteria	Commercial	10^{12} CFU mL^{-1}/2 months	Pacific white shrimp	Probiotic administration modified the bacterial community in shrimp intestine	Vargas-Albores et al. (2017)

Table 2 (*continued*)

Bacillus species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
B. subtilis and B. licheniformis	Commercial	10^4 and 10^8 g^{-1}/60 days	Pacific white shrimp	↑ Growth performance, body composition (dry matter, crude protein and ash), total protein, lysozyme and hemocyte counts ↓ serum glucose and cortisol levels	Madani, Adorian, Farsani, and Hoseinifar (2018)

N/A – no information available.
↑ - positive effect; ↓ - negative effect; → - no effect.
[a] – studies discussed in the review of Soltani et al. (2019).

lipids to be added as top.

vi) Lyophilization or freeze drying, is a low temperature dehydration process, involving freezing of the product at low pressure, and removing the ice by sublimation. This method is from time to time used in probiotic studies of finfish and shellfish (e.g. Adel, El-Sayed, Yeganeh, Dadar, & Giri, 2017a; Boonthai, Vuthiphandchai, & Nimrat, 2011; De la Banda et al., 2012; Nimrat, Boonthai, & Vuthiphandchai, 2011; Rengpipat, Phianphak, Piyatiratitivorakul, & Menasveta, 1998a).

vii) Administration – continuously or regular intervals? Most studies carried out have continuously fed the host animal for a wide range of time, varying from 15 to 94 days (Hai, 2015), but information is available on continuous or pulse-feeding of probiotic bacteria in Pacific white shrimp (Kesselring et al., 2019). The continuously application of probiotic cells (LAB, *Bacillus* spp. and certain Gram-negative spp.) may lead to high levels of colonization of the supplemented bacteria, and modulation of the gut microbiota. However, an important question arises; are the probiotics permanently colonisers in the GI tract?

viii) Co-administration of probiotics with prebiotics or plant products.

Important questions when discussing probiotics are; species isolated from the host, host specificity, strains from other species or commercial probiotics?

3. Mods of actions

Selection of potential probiotic strains is based on many different criteria, such as growth in mucus, acid and bile tolerance, survival in gastric juice, produce extracellular enzymes, produce antimicrobial substances which inhibit *in vitro* growth of pathogens, and bio-safety (hemolytic activity and antibiotic susceptibility).

i) Adhesion to the intestinal mucosa is considered an important selection criterion for persistent beneficial effects of probiotics, and is a prerequisite (Ouwehand et al., 1991; Rinkinen, Mättö, Salminen, Westermarck, & Ouwehand, 2000).

ii) Competitive exclusion, probiotic organism colonizes the gut thereby inhibiting adherence and colonization of pathogenic bacteria (Ringø et al., 2010), by producing inhibitory substances which hinder pathogenic organism to adhere and colonize the GI tract (Ringø et al., 2018; Soltani et al., 2019).

iii) Substances produced by probiotics act as antagonist for quorum sensing mechanism.

iv) Enzymatic contribution to digestion, as shown in several studies in Tables 1–3.

v) Competition for iron. For pathogenic bacteria, the ability to acquire iron is vital to survival in the host. In consequence, many genes involved in iron acquisition are associated with bacterial virulence. Siderophores, low molecular weight substances, produced by probiotic candidates or beneficial gut endosymbionts reduce the availability of iron for pathogenic bacteria, as siderophores has high affinity for ferric ion.

vi) Improved immunity, increase macrophage activity and antibody level. Probiotics which can enhance host immunity and disease resistance of finfish (Merrifield et al., 2010) and shrimps have gathered much interest during the last decade (Kumar et al., 2016; Tseng et al., 2009). Among probiotic bacteria, LAB and *Bacillus* species are most frequently used, and they have shown to promotes the health of the host animal by stimulating the innate immune response and improving resistance towards pathogenic microbial infection (Laranja et al., 2017; Rengpipat, Rukpratanporn, Piyatiratitivorakul, & Menasveta, 2000; Ringø et al., 2018; Soltani et al., 2019).

vii) Antiviral effect. The first study demonstrating bacteria with antiviral activity against infectious hematopoietic necrosis virus

Table 3

Effect of *Alteromonas, Arthrobacter, Bifidobacterium, Clostridium, Microbacterium, Paenibacillus, Phaeobacter, Pseudomonas, Pseudoalteromonas, Rhodosporidium, Roseobacter, Streptomyces, Vibrio* and combination of several potential probiotics on growth performance, immune response and disease resistance in shrimp culture.

Bacterial species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Aeromonas media	N/A	10^4 CFU mL^{-1}/5 days	Pacific oyster (*Crassostrea gigas*)	↑ Disease resistance against *V. tubiashii*	Gibson et al. (1998)
Strain CA2, probably an *Alteromonas*	N/A	10^4, 10^5, 10^6 and 10^7 CFU mL^{-1}/20 days	Pacific oyster	↑ Growth and survival	Douillet and Langdon (1994)
Arthrobacter XE-7	Culture water of Chinese white shrimp	10^6 CFU mL^{-1}/14 days	*P. chinensis*	↑ Total numbers of culturable bacteria in water, NH$_3$-N and NO$_3$-N → Survival	Li et al. (2006)
Arthrobacter XE-7	Culture water of Chinese white shrimp	10^6, 10^8, and 10^{10} CFU g^{-1}/63 days	Pacific white shrimp	↑ Total hemocyte counts, percentage phagocytosis, respiratory burst activity, serum phenoloxidase activity and disease resistance against *V. parahaemolyticus*	Li et al. (2008)
Arthrobacter sp. CW9	Intestine of Pacific white shrimp	10^5, 10^6 and 10^7 CFU mL^{-1}/24 days	Pacific white shrimp	↑ Survival rates, mean shrimp weights, phenoloxidase activity, phagocytic activity and clearance efficiency	Xue et al. (2016)
Arthrobacter enclensis	Water column of Pacific white shrimp	10^9 CFU g^{-1}/4 days	Pacific white shrimp	↑ Survival	Xue et al. (2016)
Bifidobacterium (peptidoglycan)	N/A	0.2 mg kg^{-1} shrimp BW day^{-1}/95 days	Kuruma shrimp (*Penaeus japonicus*)	↑ Disease resistance against white spot syndrome baculovirus and phagocytic activity of granulocytes → Body weight	Itami et al. (1998)
Clostridium butyricum	Commercial	10^9 CFU kg^{-1} [0, 0.25 (CB1), 0.5 (CB2) or 1.0% (CB3)]/56 days	Pacific white shrimp	↑ Growth performance, intestinal structure, digestive enzyme and SCFA content, intestine immune function of Pacific white shrimp resistance to ammonia stress and body crude protein content	Duan et al. (2017)
Clostridium butyricum	Culture collection	0, 10^7–10^{12} CFU kg^{-1}/42 days	Pacific white shrimp	↑ Specific growth rate, feed conversion ratio, intestinal villi height and intestinal wall thickness. Activities of alkaline phosphatase, acid phosphatase, lysozyme and total nitric oxide synthase in serum. Disease resistance against *V. parahaemolyticus* → Superoxide dismutase	Li et al. (2019a)
C. butyricum	Culture collection	10^{11} CFU kg^{-1}/42 days	Pacific white shrimp	↑ Specific growth rate, feed conversion ratio, intestinal villi height and intestinal wall thickness in mid intestine and disease resistance against *V. parahaemolyticus*. The relative expression levels of superoxide dismutase, lysozyme, prophenoloxidase, Toll, immune deficiency, relish, TOR, 4E-BP, eIF4EIα and eIF4E2 genes	Li et al. (2019b)
C. butyricum	Commercial	10^7 CFU kg^{-1}/42 days	Marron (*Cherax cainii*)	↑ Growth, total haemocyte counts and lysozyme activity in haemolymph, and protein content in tail muscle Probiotic feeding modulate the hindgut microbiota ↓ Vibrio and Aeromonas counts in the hindgut microbiota.	Foysal et al. (2019)
Microbacterium aquimaris	Water column of Pacific white shrimp	10^9 CFU g^{-1}/4 days	Pacific white shrimp	↑ Survival	Xue et al. (2016)
Paenibacillus	Marine sediment	10^4 and 10^5 CFU ml^1/1 day	Giant tiger prawn	↑ Disease resistance against *V. harveyi*	Ravi et al. (2007)
Phaeobacter gallaeciensis	Water column of Pacific white shrimp	10^9 CFU g^{-1}/4 days	Pacific white shrimp	↑ Survival	Xue et al. (2016)
Phaeobacter sp. S4	Marine environment	10^4 CFU mL^{-1}/1 day	Eastern oyster (*Crassostrea virginica*)	↑ Disease resistance against *V. tubiashii*	Karim et al. (2013)
Phaeobacter daeponensis	N/A	3–5 x 10^{10} CFU g^{-1}/180 days	Abalone	↑ Shell length, wet weight, glutathione peroxidase-, catalase-, alkaline phosphatase-, acid phosphatase- and superoxide dismutase activities, disease resistance against *V. harveyi* Modulate gut microbiota	Zhao et al. (2018)
Phaeobacter inhibens	N/A	10^4 and 10^6 CFU mL^{-1}/2 days	Bay scallop (*Argopecten irradians*)	↑ Disease resistance against *V. coralliilyticus*	Sohn et al. (2016)

(continued on next page)

Table 3 (continued)

Bacterial species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Pseudomonas PS-102	Muttukkadu brackish water lagoon	10^7 CFU mL^{-1}/5 days	Giant tiger prawn	Not pathogenic to Giant tiger prawn larvae. No challenge test with pathogens was carried out	Vijayan et al. (2006)
Pseudomonas aestumarina	Intestine of adult Pacific white shrimp	10^5 CFU g^{-1}/28 days	Pacific white shrimp	↑ Survival, final weight, feed conversion ratio and disease resistance against *V. parahaemolyticus*	Balcázar et al. (2007)
Pseudomonas synxantha and *Pseudomonas aeruginosa*	Commercial	10^5 CFU mL^{-1}/84 days	Western king prawn (*Penaeus latisulcatus*)	↑ FCR → Survival and specific growth rate	van Hai et al. (2009b)
Pseudoalteromonas sp. X153	Marine environment	10^6 CFU mL^{-1}/duration N/A	*Pecten maximus*	Administration of probiotics, enhanced the number of probiotics in intestine of prawn and lower the bacteria numbers in haemolymph. ↑ Disease resistance against *Vibrio* sp.	Longeon et al. (2004)
Pseudoalteromonas sp. NC201	Marine environment	1.39×10^5 CFU mL^{-1}/2 days	*Litopenaeus stylirostris*	↑ Survival by hyposaline stress and disease resistance against *V. nigripulchritudo*	Sorieul et al. (2018)
Pseudoalteromonas CDM8 and CDA22	Hindgut of Pacific white shrimp	10^7 CFU g^{-1}/28 days	Pacific white shrimp	↑ Disease resistance against *V. parahaemolyticus* ↓ Viable *Vibrio* counts in hindgut	Wang et al. (2018)
Rhodobacter sphaeroides and *B. coagulans*	Intestine of common carp (*Cyprinus carpio*)	~10^8 CFU and 10^9 CFU g^{-1}/28 days	Pacific white shrimp	↑ Growth and intestinal protease, amylase, lipase and cellulase activities	Wang (2007)
Rhodosporidium paludigenum	Costal water	10^8 CFU g^{-1}/42 days	Pacific white shrimp	↑ Growth performance, antioxidant competence, and digestive activities. Modulate the intestinal microbiota	Yang et al. (2010)
Roseobacter BS107	Marine environment	10^6 CFU mL^{-1}/25 days	*Pecten maximus*	↑ Survival	Ruiz-Ponte et al. (1999)
Roseobacter gallaeciensis	Intestine of adult Pacific white shrimp	10^5 CFU g^{-1}/28 days	Pacific white shrimp	↑ Survival, final weight, feed conversion ratio and disease resistance against *V. parahaemolyticus*	Balcázar et al. (2007)
Shewanella algae IPA-S.252	Hepatopancreas/stomach of Pacific white shrimp	10^6 CFU g^{-1}/45 days	Pacific white shrimp	→ FW *Vibrio* counts in hepatopancreas decreased during probiotic feeding, while *Vibrio* counts in intestine and faeces increased	Interaminense et al. (2018)
Streptomyces sp.	Marine sediment from a shrimp farm	1% cell mass/15 days	Giant tiger prawn	↑ Growth and disease resistance against *V. harveyi*	Das et al. (2010)
Streptomyces sp. N7 and RL8	Marine sediment	10^8 bacteria g^{-1}/30 days	Pacific white shrimp	↑ Higher hemocyte count and disease resistance against *V. parahaemolyticus* by RL8 administration → Growth performance by N7 and RL8 administration. ↓ Reduction of *Vibrio* from hepatopancreas	García Bernal et al. (2017)
Streptomyces fradiae	Mangrove sediment	10^6 bacteria mL^{-1} rearing water, and 10^9 bacteria g^{-1}/ Duration N/A	Giant tiger prawn	↑ Growth performance, best effect by dietary supplementation	Aftabuddin et al. (2013)
Streptomyces rubrolavendulae M56	Sediment of bay of Bengal	Dose N/A/28 days	Giant tiger prawn	↑ CFU and viable *Vibrio* counts per mL rearing water ↑ Survival → Total heterotrophic bacterial counts in culture system ↓ Viable *Vibrio* sp. counts in culture system	Augustine et al. (2016)
Vibrio alginolyticus	Intestine of adult Pacific white shrimp	10^5 CFU g^{-1}/28 days	Pacific white shrimp	↑ Final weight, feed conversion ratio and disease resistance against *V. parahaemolyticus* → Survival during probiotic feeding	Balcázar et al. (2007)
Vibrio NE17	N/A	4.34×10^9 CFU g^{-1}/60 days	Giant freshwater prawn (*M. rosenbergii*)	↑ Specific growth rate, weight gain, survival, water quality parameters, total haemocyte counts, phenoloxidase and respiratory burst	Rahiman et al. (2010)
Combination of bacteria					
Bacillus sp. and *Saccharomyces* sp.	Commercial	10^8 CFU of *Bacillus* and 5.6×10^5 CFU of *Saccharomyces* mL^{-1}/110 days	Giant tiger prawn	Lower concentration in total ammonia N, nitrate, chemical oxygen demand and biological oxygen demand	Matias et al. (2002)

Table 3 (continued)

Bacterial species	Isolated from	Doses/duration	Shellfish species	Parameters investigated	References
Bacillus, Nitromonas, Nitrobacter and *Saccharomyces cerevisiae*	Commercial	10^9 *Bacillus* mL^{-1}, *Nitrobacter* 2.8 × 10^6 CFU mL^{-1}, *Nitromonas* 6.4 × 10^4 CFU mL^{-1} and *S. cerevisiae* 4.5 × 10^5 mL^{-1}/101 days	Giant tiger prawn	↑Yields of shrimp ↓Concentrations of nitrogen and phosphorus	Wang et al. (2005)
N/A	Commercial	Dose N/A/138 days	Giant tiger prawn	↑Final body weight, survival and water quality	Hossain, Kamal, Mannan, and Bhuyain (2013)
S. phocae and *B. subtilis*	Commercial	4.6 × 10^8 CFU mL^{-1}/30 days	Giant tiger prawn	↑Total hemocyte counts, phenol oxidase-, phagocyte activities, respiratory burst and resistance against *V. parahaemolyticus*	Pattukumar et al. (2013)
Zymetin (*B. mesentericus, C. butyricum* and *Ent. faecalis*)	Commercial	5 g kg^{-1}/60 days	Freshwater prawn (*Macrobrachium rosenbergii*)	↑Total haemocyte count in the haemolymphs, resistance against *Vibrio* spp. and *Aeromonas* spp. Modulate the culturable bacteria in water and intestine	Azad et al. (2019)
Lb. pentosus, Lac. fermentum, Bacillus subtilis, *Saccharomyces cerevisiae*	Commercial probiotic	10^7, 10^8 and 10^9 CFU kg^{-1} diet/56 days	Pacific white shrimp	↑Growth performance, survival rate, resistance against *V. parahaemolyticus* →Carcass composition	Wang et al. (2019b)

↑ - positive effect; ↓ - negative effect; → - no effect.

(IHNV) was carried out (Kamei, Yoshimizu, Ezura, & Kimura, 1987). Since then, some studies were carried out, 1988–1995. However, the topic lost interest. However, more recently, is has been revealed that probiotic administration controlling viral diseases (Lakshmi, Viswanath, B., & SaiGopal, 2013).

viii) Improve water quality in ponds through modulation of the water microbiota (Cai et al., 2019), improve water physicochemical parameters (Zokaeifar et al., 2014), and control diseases (Kuebutornye et al., 2019).

4. Lactic acid bacteria

Lactic acid bacteria (LAB) have gained much attention as probiotics in aquaculture, for review see the comprehensive review of Ringø et al. (2018). They belong to phylum Firmicutes, class Bacilli and order Lactobacillales, and are Gram-positive, non-endosporing with rod- or coccid morphology. LAB are catalase- and oxidase negative, and most of them are non-motile with a growth optimum at pH 5.5–5.8. They are divided into homofermentative, produce lactic acid from sugars, or heterofermentative, produce lactic acid, acetic acid or alcohol and carbon dioxide. Another favourable trait of LAB is that they produce antimicrobial substances, bacteriocins (e.g. Cotter, Hill, & Ross, 2005; Klaenhammer, 1993; Ringø et al., 2018).

When discussing probiotics, host specificity of LAB is a topic to mention. Previously, adhesion of probiotic LAB was reported to be host specific, and Fuller (1989) stated, "*The attachment to epithelial cells is very host specific which means in practical terms that a strain which is suitable as pig probiotic may not be active in chick and other animals*". However, several later studies have indicated that LAB originated from one host, adhere to mucus of other species (e.g. Nikoskelainen, Ouwehand, Salminen, & Bylund, 2001b; Nikoskelainen, Salminen, Bylund, & Ouwehand, 2001a; Rinkinen et al., 2000; Rinkinen, Westermarck, Salminen, & Ouwehand, 2003; Tuomola, Ouwehand, & Salminen, 1999). In addition, adhesion ability of LAB may be related to; adhesive and non-adhesive ability (Zhou et al., 2012), variation of mucin adhesion and cell surface characteristics depending on their isolation habitats indicated by Buntin, de Vos, and Hongpattarakere (2017), and hydrophobic properties (Grajek, Sip, Foksowicz-Flaczyk, Dobrowolska, & Wita, 2016).

There are many reports regarding the advantages of using LAB as probiotics in shellfish aquaculture (Table 1).

4.1. Enterococcus faecium

Swain, Singh, and Arul (2009) administered *E. faecium* at 10^7 CFU g^{-1} to giant tiger prawn (*Penaeus monodon*) for unknown numbers of days and exposed the shrimp to *Vibrio harveyi* and *Vibrio parahaemolyticus*, and revealed improved resistance against the pathogens. In a later study, Sha et al. (2016a) revealed that *E. faecium* had high adhesive activity, and improved expression of immune and digestion related genes in the mid gut of shrimp.

4.2. Lactobacillus sp

A mixture of *Lactobacillus* spp. isolated from chicken GI tracts improved the growth and survival rates of juvenile tiger shrimp when fed with *Lactobacillus* strains for 100 days (Phianphak, Rengpipat, Piyantiratitivorakul, & Menasveta, 1999). Karthik, Jaffar, and Muthezhilan (2014) isolated a *Lactobacillus* sp. AMET1506 strain from curd which displayed strong antibacterial activity towards the pathogenic bacteria, *V. harveyi*. The lactobacilli was included in a diet at 10^6 CFU g^{-1} and fed to Pacific white shrimp for 30 days, and thereafter challenged with *V. harveyi* at a dose of 10^5 CFU mL^{-1} for 10 days. The shrimp fed the lactobacilli diet revealed improved weight gain *vs.* shrimp fed the control diet; not supplemented by *Lactobacillus*. As expected, dietary supplementation of *Lactobacillus* increased the

Lactobacillus count in Pacific white shrimp intestines, but an important finding revealed was a significantly decrease in the bacterial load of *Vibrio*. Based on their results, the authors suggested that *Lactobacillus* AMET1506 could be a potential probiotic for Pacific white shrimp by modulation of the gut microbiota to control vibriosis in Pacific white shrimp farming. This suggestion was later confirmed as total heterotrophic bacterial load and LAB counts in intestine increase, while the bacterial load of *E. coli*, *Salmonella* spp. and *Shigella* spp. in intestine declined by feeding Pacific white shrimp 10^5 *Lactobacillus* sp. AMET1506 (Karthik, Pushpam, Chelevan, & Vanitha, 2015). Recently, Zuo, Shang, Shao, Li, and Sun (2019) conducted a 28-day feeding trial of Pacific white shrimp, and a WSSV infection trial to determine the effects of *Lactobacillus* sp. on the growth, health status, and disease resistance. The results showed that during probiotic administration, the body weight of shrimp enhanced, and the activities of immune enzyme and digestive enzyme of shrimp fed with probiotics increased. After probiotic feeding, the cumulative mortality of the probiotics groups were significantly lower than the control group after WSSV infection. Moreover, electron microscopy evaluation of the midgut revealed that the intestinal mucosa was tight and the epithelium cells displayed an active secretory state in probiotics group. Furthermore, evaluation of the intestinal microbial communities revealed that probiotic administration affected the microbial community, and that the ability of intestinal microorganism to utilize carbon source was significantly enhanced, which may indicate that the digestive enzyme secreted by probiotics can improve digestion and absorption rate, thus promoting the rapid growth of shrimp.

4.3. Lactobacillus acidophilus

In a study with juvenile tiger shrimp, *Lb. acidophilus* 04 (10^5 CFU g^{-1}) was administered for one month and increased resistance (80% survival) was observed following exposure with *Vibrio alginolyticus*; 10^5 CFU mL^{-1} after 10 days challenge (Sivakumar, Sundararaman, & Selvakumar, 2012). Later, Khan and Mahmud (2015) addressed the effect of *Lb. acidophilus*, and revealed improved growth and survival of the juvenile giant fresh water river prawn (*Macrobrachium rosenbergii*) infected with pathogenic *Vibrio* spp.

4.4. Lactobacillus brevis

Karthik and Bhavan (2018) conducted a 90-day feeding trial to determine the effects of probiotic effect of *Lb. brevis*, and revealed significant improvement of growth performance, digestive enzymes (protease, amylase and lipase) and body composition. Furthermore, probiotic administration modulated the gut microbiota.

4.5. Lactobacillus bulgaricus

In an early study, Ajitha, Sridhar, Sridhar, Singh, and Varghese (2004) supplemented Indian white shrimp (*Penaeus indicus*) diet with as single dose (5×10^6 CFU g^{-1}) of *Lb. bulgaricus*-57 for 4 weeks, and at the end of feeding trial was shrimp intra-muscular injected with 0.1 mL of an inoculum of 3×10^9 *V. alginolyticus* per mL. The results revealed improved mortality rate (40%) compared control group (20%). In a recent study, Roomiani, Ahmadi, and Ghaeni (2018) administered a *Lb. bulgaricus* isolated from Pacific white shrimp intestine to Pacific white shrimp at two inclusion levels; 10^7 and 10^9 CFU g^{-1}, for 30 days and challenged with *V. parahaemolyticus*. There was significant enhancement of hemocyte counts, phenoloxidase activity, respiratory burst, and improved disease resistance against the pathogen, but it's worth noticing that the best results were revealed at inclusion level of 10^9 CFU g^{-1}.

4.6. Lactobacillus pentosus

The potential of *Lb. pentosus* as probiotics in shellfish aquaculture has been investigated in three studies (Gao et al., 2018; Sha et al., 2016c, 2016a). Sha et al. (2016a) reported that administration of 10^7 *Lb. pentosus* g^{-1}, survival, adhesive activity, expression of PEN-3α, proPO, trypsin and α-amylase in the midgut, and proPO, LGBP, IveLee, trypsin and α-amylase in the hepatopancreas in Pacific white shrimp. Sha et al. (2016c) used a *Lb. pentosus* strain isolated from intestine of healthy *Acanthogobius hasta* to evaluate the probiotic administration on bacterial community in intestines of Pacific white shrimp and intestinal histology. The abundance of intestinal Actinobacteria increased, while no improvements of intestinal histology were revealed. In a recent study, Gao et al. (2018) revealed that inclusion of *Lb. pentosus* at 10^3 CFU g^{-1} and 10^5 CFU g^{-1}, significantly improved survival rate, shell length-specific growth rate and feed conversion rate of abalone (*Haliotis discus hannai* Ino) compared to control. In groups fed *Lb. pentosus*, total number of blood lymphocytes, lysozyme activity, acid phosphatase, superoxide dismutase, and expression levels of Mn-superoxide dismutase and thioredoxin peroxidase increased vs. the control, in contrast malondialdehyde content. The probiotic effect on disease resistance was tested by infection of *V. parahaemolyticus*. At day seven all abalones in the control group were dead, while survival was significantly improved in the *Lb. pentosus* added groups. Based on their results, the authors concluded that *Lb. pentosus* originally isolated from the intestinal tract of abalone is a promising probiotic strain in abalone culture, but its potential in other shellfish species merits investigations.

4.7. Lactobacillus plantarum

Lb. plantarum has gained popularity in fish and shellfish farming, and in an early study by Chiu Sundararaman and Selvakumar (2007) *Lb. plantarum* were reported to enhance the immune responses and gene expression in Pacific white shrimp. The bacteria influenced both the cellular and humoral immune defences in the shrimp. *Lb. plantarum* enhanced the phenoloxidase - and prophenoloxidase activities, respiratory bursts, superoxide dismutase activity and clearance efficiency of *V. alginolyticus*, peroxinectin mRNA transcription, and survival rate of Pacific white shrimp after challenged with *V. alginolyticus* when the diet containing 10^{10} *Lb. plantarum* kg^{-1} diet for 168 h. Similarly, Vieira et al. (2007) used *Lb. plantarum* as probiotic in Pacific white shrimp diet, and revealed that the dietary supplementation improved larval survival and enhanced resistance to *V. harveyi*. In a later study, Vieira et al. (2010) administered a *Lb. plantarum* to Pacific white shrimp for 60 days, and examined the following intestinal bacteria; total bacterial counts, total *Vibrio* counts and total LAB counts by cultivation. After 60 days, the probiotic supplemented diet significantly decreased total bacterial counts and total *Vibrio* counts, and enhanced total LAB counts. The latter finding is not surprisingly as feeding was not reverted back to a control diet without LAB supplementation. Therefore, in future studies the intestinal microbiota should be investigated post probiotic administration, for example 4 weeks. Moreover, probiotic administration significantly increased the resistance against *V. harveyi* infection in Pacific white shrimp. After challenge, the bacterial counts in haemolymph and hepatopancreas was significantly lower by probiotic administration, while total hemocyte counts and serum agglutination activity were significantly higher. Subsequently, the effect of *Lb. plantarum* administration fed to fresh water river prawn was investigated by Rahiman, Jesmi, Thomas, and Hatha (2010), and revealed significant enhancement of specific growth rate, weight gain and phenoloxidase. However, probiotic feeding did not significantly improved survival, total haemocyte counts or respiratory burst.

A commercial product containing *Lb. plantarum*, at 3.3×10^{11} CFU g^{-1} feed, at inclusion of 0, 0.001, 0.01, 0.1 and 1 g^{-1} was fed to post larval Kuruma shrimp (*Marsupenaeus japonicus*) for 30 days (Tung, Koshio, & Traifalgar, 2010). Growth performance and stress

resistance were improved at 1 g inclusion, while 0.1 g^{-1} showed highest relative survival. Moreover, no difference was noticed in protease activity between the treatments.

Kongnum and Hongpattarakere (2012) revealed that *Lb. plantarum* isolated from the shrimp intestines, no specification was given, significantly improved relative growth rate, feed conversion ratio, survival rate, and haemocytes count as well as disease resistance to *V. harveyi* in Pacific white shrimp. Talpur, Ikhwanuddin, Daniel Abdullah, and Ambok Bolong (2013) investigated the effect of *Lb. plantarum* administration at three inclusion levels, 10^6, 5×10^6 and 10^7 CFU mL^{-1}, on blue swimming crab (*Portunus pelagius*), and revealed best effect by 5×10^6 administration; improved survival, protease – and amylase activities. Not surprisingly, the total bacterial- and *Vibrio* counts in tank water was significantly lower in treated tanks *vs.* control, while probiotic administration revealed no clear effect on nitrogen content and pH of culture water. In three later studies using tiger shrimp, Dash et al. (2014, 2015, 2016) revealed that dietary inclusion of *Lb. plantarum* significant increased weight gain, specific growth rate, feed conversion efficiency, protein efficiency ratio, and carcass protein content, whereas feed conversion ratio significant decreased. During probiotic feeding, LAB counts significantly increased in the intestine with a concurrent decrease in Gram-negative bacteria counts. However, as the LAB counts decreased after switching back to basal diet, this clearly indicated that a *Lb. plantarum* from a culture collection was not able to permanently colonize the intestine of Pacific white shrimp. On the other hand, immune parameters analysis revealed significantly improvement in total hemocyte count, phenol oxidase- and respiratory burst activities and resistance against *Aeromonas hydrophila*.

A dietary supplementation of a *Lb. plantarum* isolated from Pacific white shrimp (Vieira et al., 2007) was administrated to Pacific white shrimp for 4 weeks days and challenged with *V. alginolyticus* (Ramirez et al., 2017). There was significant enhancement of phenoloxidase activity, intestinal LAB and resistance against *V. alginolyticus*. However, growth performance, total heterotrophic bacteria in intestine and intestinal *Vibrio* counts increased, which implicate that *Lb. plantarum*, even though the bacterium was isolated from the host, was not able to outcompete *Vibrio* already present in the intestine, or that the administration period was too short. In later study using host-derived *Lb. plantarum*, Chomwong, Charoensapsi, Amparyup, and Tassanakajon (2018), revealed significant enhancement in haemolymph PO activity, relative mRNA expression of *Lv*proPO1, *Lv*proPO2, and resistance against *V. parahaemolyticus*. Even though information was presented by cultivation - and scanning electron microscopy analysis after 16 days of probiotic administration and 5 days post probiotic feeding, revealed presence of LAB in the intestine- These findings do not confirm permanent colonization, only indicating temporary colonization. However, no information was presented whether post probiotic administration affected the gut microbiota. Recently, Zheng, Duan, Dong, and Zhang (2017) administrated four treatments of a commercial *Lb. plantarum*, fermentation supernatant (FS), live bacteria (LB), dead bacteria (DB) and cell-free extract (CE) of *Lb. plantarum* for 45 days to Pacific white shrimp. The results revealed that probiotic administration significant enhanced final weight, WG, SGR, FCR, digestive enzyme activities and enterocytes height, improved resistance against stress, acute low salinity, but revealed no significant effect on gene expression of superoxide and lysozyme. Based on their results, the authors suggested that especially the CE diet might be a potential feed additive to overcome environmental stress of shrimp. Similar conclusion was shown in a later study, as Zheng, Duan, Dong, and Zhang (2018) administrated the FS, LB, DB and the CE diets for 15 days to Pacific white shrimp, and reported that probiotic administration significant enhanced final weight. Significantly highest weight gain and specific growth rate, and the highest lipase, amylase and pepsin activities in hepatopancreas and intestine were noticed for the CF diet. However, the above mention studies, did not evaluate the effect on gut microbiome and resistance towards pathogens, topics merits investigations.

Two strains of *Lb. plantarum* T8 and T13 was fed to Pacific white shrimp for 3 weeks, and then 7 weeks without probiotic feeding prior to challenge with *V. parahaemolyticus* (Nguyen et al., 2018). There was significant enhancement of growth and disease resistance towards the pathogen by feeding T8, while T13 revealed better disease resistance compared to the T8 treatment, but no growth improvement was noticed. The results are of interest, but further studies are needed as only a short period, 3 weeks, of probiotic feeding was used.

Good management practice might masked the possible effect of probiotic supplementation on the water quality, as Correa et al. (2018) revealed that dietary inclusion of *Lb. plantarum* had no effects on water quality and pathogens removal in Pacific white shrimp culture under biofloc system. In contrast, dietary inclusion of *Lb. plantarum* significantly improved water quality and reduced shrimp diseases, as well as environmental impact (Pacheco et al., 2018).

Dietary *Lb. plantarum* at inclusion levels of 0, 10^7 (LB7), 10^8 (LB8), and 10^9 (LB9) CFU g^{-1} diet was fed to clawed crayfish (*Astacus leptodactylus*) for 97 days (Valipour, Nedaei, Noori, Khanipour, & Hoseinifar, 2019). There was significant enhancement of total haemocyte count, semi granular cells, hyaline cells count, total plasma protein and phenoloxidase by LB7 and LB8 administrations, while superoxide dismutase and catalase increased by LB7 administration. The LB8 and LB9 administration significantly elevated protease-, amylase- and alkaline phosphatase activities. Some bacterial assessments were carried out, and the results displayed no effect on autochthonous intestinal bacteria counts. Moreover, as expected the autochthonous LAB levels were significantly elevated in all probiotic treatments, and the highest levels were revealed in treatments LB8 and LB9. However, permanent colonization was not evaluated.

4.8. Lactobacillus sporogenes

Seenivasan, Radhakrishnan, Shanthi, Muralisankar, and Saravana Bhavan (2014) conducted a study with fresh water river prawn fed *Lb. sporogenes* for 90 days, and revealed significantly improved growth performance, total protein, total free amino acid, total carbohydrate, and total lipid content; as well as feeding rate, absorption rate, conversion rate, and excretory rate.

4.9. Mixture of LAB

Phianphak et al. (1999) revealed that a mixture of *Lactobacillus*, including *Lb. acidophilus*, *Lb. bulgaricus*, *Lb. casei*, *Lb. casei* subsp. *tolerans* and *Lb. jensenii* originally isolated from the GI tract of chicken improved the growth and survival rates of juvenile tiger shrimp exposed to *V. harveyi* when fed the lactobacilli strains for 100 days. A multi-strain probiotic, PrimaLac© (*Lb. acidophilus, Lb. casei, E. faecium* and *B. bifidium*) was fed at 0, 0.25, 0.5 and 1 g kg^{-1} to Pacific white shrimp for 60 days (Miandare, Yarahmadi, & Abbasian, 2016), and generally, there was significant enhancement of weight gain, SGR, body, body crude protein, FCR, protease, amylase, lipase and penaeidin gene expression, in contrast to the decrease of body crude lipid and body moisture. Other studies have also evaluate the combination of several probiotics in Pacific white shrimp diets, such as *E. faecium*, and *Lb. pentosus* (Sha et al., 2016a; 2016b), or combination of *Lb. pentosus*, *Lac. fermentum*, *B. subtilis*, and *S. cerevisiae* (Wang, Hu, Chiu, & Liu, 2019), and these studies revealed significantly enhanced disease resistance against *V. parahaemolyticus*.

4.10. Lactococcus garvieae

Lac. garvieae at inclusion level of 10^7 CFU g^{-1} was fed to tiger shrimp and challenged with *V. harveyi* and *V. parahaemolyticus* (Swain et al., 2009). For *V. harveyi*, 40% survival was revealed, while approximately 15% was noticed in the *V. parahaemolyticus* study.

4.11. Lactococcus lactis

Maeda et al. (2014) conducted a 7 day feeding trial and a subsequent 24 h challenge trial to determine the effects of *Lac. lactis* on the health status, and disease resistance of kuruma shrimp (*Marsupenaeus japonicus*). There was significant enhancement of up regulation of lysozyme gene expression in intestine and hepatopancreas, and resistance against *V. penaeicida*. However, anti-lipopolysaccharide factor, superoxide dismutase, prophenoloxidase and toll-like receptor in intestine was not enhanced by probiotic administration. Adel et al. (2017a) revealed that administration of 10^7 and 10^8 CFU g^{-1} of *Lac. lactis* to Pacific white shrimp for 8 weeks enhanced growth rate, survival, body protein level, and the digestive enzymes (cellulase, lipase, amylase and protease). Furthermore, intestinal bacterial levels of *Lactobacillus* and *Bacillus* were significantly enhanced by probiotic administration, in contrast to *Vibrio* counts which decreased. In addition, probiotic administration improved disease resistance against *V. anguillarum*. Host-derived feeding of *Lac. lactis* supplemented at a final concentration of 2–4 x 10^8 CFU g^{-1} feed to Pacific white shrimp for 16 days and challenged with *V. parahaemolyticus* was investigated by Chomwong et al. (2018). The results revealed significant enhancement of haemolymph PO activity, relative mRNA expression of *Lv*proPO1, *Lv*proPO2, temporary colonization of the *Lactococcus* in the GI tract, and resistance against *V. parahaemolyticus*.

4.12. Pediococcus acidilactici

P. acidilactici showed an effect on antioxidant defence and oxidative stress of Pacific white shrimp when challenged with *Vibrio nigripulchritudo*. Probiotic administration was effective on the antioxidant defences, superoxide dismutase, catalase, glutathione peroxidase, total antioxidant status, glutathione's, and induced tissue damage, and *P. acidilactici* was efficient in maintaining the antioxidant defence levels for a longer period than the control and uninfected groups (Castex, Lemaire, Wabete, & Chim, 2010). This findings suggests that probiotic bacteria besides enhancing the immune defences also maintain the defence levels in the shrimp offering a prolonged protection. When discussing commercial probiotic product, it's worth to mention that *P. acidilactici* MA 18/5M was one of the first officially commercial probiotic product approved for use in fish aquaculture in Europe (Feed Additive Magazine, September 28, 2012). However, since then are 29 commercial products available on the marked for shellfish and finfish (Cordero et al., 2014).

4.13. Streptococcus cremoris

In the study of Ajitha et al. (2004), the authors also fed the Indian white shrimp with as single dose (5×10^6 CFU g^{-1}) of *S. cremoris* for 4 weeks, and at the end of feeding trial was shrimp intra-muscular injected with 0.1 mL of an inoculum of 3×10^9 *V. alginolyticus* per mL, and a mortality rate of 20% was revealed. This rate was lower than that of shrimp fed *Lb. bulgaricus*-57 (40%) and shrimp fed the control diet (80%).

4.14. Streptococcus phocae

In an early study, Swain et al. (2009) revealed that administration of *S. phocae* to tiger shrimp improved specific growth rate and resistance against *V. harveyi*. In addition, it is of interest to notice that *S. phocae* exhibited higher resistance, 94% survival, compared to the other probiotics used, *E. faecium* (84%), *Lac. garvieae* (40%) and a commercial probiotic (68%). Pattukumar et al. (2013) evaluated the effect of commercial *S. phocae* to tiger shrimp for 30 days and challenged with *V. parahaemolyticus*, and revealed significant increase in total hemocyte counts, phenol oxidase-, phagocyte activities, respiratory burst and resistance against *V. parahaemolyticus*.

4.15. Synbiotic studies

Synbiotic, combination of pro- and prebiotics, studies are well known in finfish aquaculture (Ringø & Song, 2016), but is less investigated in shellfish aquaculture. However, in a recent study, the effect of a synbiotic diet, galactooligosaccharide and *Lb. plantarum* was administrated to Pacific white shrimp for 60 days and challenged with *V. alginolyticus* (Huynh, Cheng, Chi, Chiu, & Liu, 2018). There was significant enhancement of immune parameters such as phenoloxidase activity, respiratory burst, phagocytic activity, prophenoloxidase I, serine proteinase and peroxinectin and survival when the shrimp were challenged with *V. alginolyticus*.

5. Bacillus sp

Species within genus *Bacillus* are Gram-positive, catalase-positive, endosporing, aerobic or facultative anaerobes, characterized by their rod-shaped morphology (between 2.5 and 10 μm), and is classified in the Phylum Firmicutes, Class Bacilli, and Order Bacillales. The genus comprises of approximately 200 bacterial species, and are almost ubiquitous in nature and they have been isolated from compost, extreme environments such as high pH conditions, at high temperature, high salt concentrations, in aquatic environments as well as in the gastrointestinal (GI) tract of aquatic animals (Soltani et al., 2019). *Bacillus* exhibit quite diverse physiological properties such as the ability to produce cellulase, phytase, tannase, chitinase, xylanase, protease and lipase (Ghosh, Ray, & Ringø, 2019; Ray, Ghosh, & Ringø, 2012), antimicrobial substances (Abriouel, Franz, Ben Omar, & Gálvez, 2011; Stein, 2005) as well as modulation of antioxidant enzymes, stress mitigation and prevent tissue damage (Kuebutornye et al., 2019). In addition, dietary supplementation of bacilli may improve digestive enzyme activities (Soltani et al, 2019). It is widely accepted, that the level of digestive enzyme activity is a useful comparative indicator of the host's food utilization rate, digestive capacity, and growth performance (Ueberschär, 1995; Suzer et al., 2008).

According to Elshaghabee, Rokana, Gulhane, Sharma, and Panwar (2017) there are 17 probiotic supplements containing *Bacillus* available in the global market. Genus *Bacillus* have been widely used as environmental probiotics (Moriarty, 1998) and dietary probiotics (Hong, Duc, & Cutting, 2005) in aquaculture due to their production of antimicrobial substances, enzymes provide and their ability to colonize the digestive tract and to contribute to nutrition of the host (Soltani et al., 2019). In addition, *Bacillus* has simple nutritional requirements, fast metabolic rate, ease to isolate and preserve, and these advantages make them to be one of the most studied probiotics in aquaculture.

In their review devoted to *Bacillus* in fish and shellfish aquaculture, Soltani et al. (2019) presented information on their potential of *Bacillus* as promising probiotics on growth performance, their effect on the immune system and disease resistance against pathogens. In order to avoid duplication, studies reviewed in the aforementioned review are only briefly addressed in the text and Table 2 in the present paper.

5.1. Bacillus sp

Giant tiger prawn (*Penaeus monodon*). Earlier studies with *Bacillus* suggested that *Bacillus* S11, a saprophytic strain, was able to enhance resistance of giant tiger prawn when challenged with *V. harveyi* (Rengpipat et al., 1998a; Rengpipat, Rukpratanporn, Piyatiratitivorakul, & Menasveta, 1998b), and in a later study, feeding live bacteria seems to be an effective treatment for improving the growth in pond condition of giant tiger prawn as Rengpipat et al. (2000) revealed that *Bacillus* S11 stimulate the immune response by activating phenoloxidase, phagocytosis and antimicrobial activity in the haemolymph of giant fresh water river prawn to improve resistance against *V. harveyi*. When giant tiger shrimp were fed with *Bacillus* S11 for 100 days, improved growth and higher resistance was seen after

challenging with *V. harveyi* (Rengpipat, Tunyanun, Fast, Piyatiratitivorakul, & Menasveta, 2003). In order to monitoring *Bacillus* S11 as probiotics in giant tiger prawn, Rengpipat, Wongtangprasert, and Palaga (2009) used green fluorescent protein, and revealed the bacterium in the intestine after 9 weeks of feeding.

Dalmin, Kathiresan, and Purushothaman (2001) demonstrated that the application of an indigenous *Bacillus* spp. in the rearing water of giant tiger prawn was able to maintain optimum transparency and low organic carbon of the pond, as well as a decrease in *Vibrio* counts in the water column. Matias, Yusoff, Shariff, and Azhari (2002) compared the efficacy of two commercial probiotic products on the water quality of commercial giant tiger prawn grow-out ponds, and relatively a lower concentration in total ammonia N, nitrate, COD and biological oxygen demand was seen in the early culture phase of ponds treated with a mixture of *Bacillus* sp. and *Saccharomyces* sp. than in ponds treated with a mixture of *Bacillus* sp., *Nitrosomonas* sp. and *Nitrobacter* sp. Additionally, no significant difference was recorded in values of salinity, ammonia, hydrogen sulphide or pH, while dissolved oxygen and transparency values were slightly increased.

Pacific white shrimp (Litopenaeus vannamei). Pacific white shrimp is one of the most important species used in aquaculture, and some studies have addressed the use of probiotic *Bacillus* sp. in Pacific white shrimp aquaculture. Feeding Pacific white shrimp with dietary *Bacillus* deceased the total viable counts of bacteria and the *Vibrio* count in the shrimp intestine (Li, Tan, & Mai, 2009), while *Bacillus* OJ enhances the immune response (phenoloxidase, phagocytosis, etc.) and provides protection against white spot syndrome virus (WSSV) in the same species (Li et al., 2009; Tseng et al., 2009).

Chai, Boonthai and Vuthiphandchai (2016) investigated the effects of *Bacillus* bacteria isolated from the intestine of a healthy, wild shrimps on the growth of Pacific white shrimp and showed that probiotics reduced shrimp culture risks from stressful conditions and improved growth total weight, specific growth rate, FCR, digestion and nutrient absorption.

Chai, Song, Chen, Xu, and Huang (2016) carried out a 30-day feeding trial and a subsequent 20-day anti-virus infection trial to evaluate the effects of *Bacillus* PC465, at inclusion level of 10^7, and 10^9 CFU g^{-1}, on growth, health status, and disease resistance of Pacific white shrimp. Probiotic administration significantly increased the weight gain and survival of the shrimp, but the effect of 10^9 CFU g^{-1} on the growth rate was higher than that of 10^7 CFU g^{-1}. Compared to the control group, activities of amylase and protease in the shrimp midgut significantly enhanced by probiotic administration. Histological evaluations by scanning electron microscopy revealed improvements by probiotic treatment. The probiotic feeding significantly enhanced the transcription of penaeidin 3a, peroxinectin, C-type lectin 3, and thioredoxin in the shrimp hemocytes. DGGE analysis of the mid-gut microbiota was modulated by probiotic treatment-fed group than in the control group, and not surprisingly the proportion of *Bacillus* in the probiotic treatment increased. Moreover, probiotic administration provided protection against viral infection. Bachruddin, Sholichah, Istiqomah, and Supriyanto (2018) reported that addition of probiotics, including *Bacillus* spp., into the culture water of Pacific white shrimp significantly improved weight gain, total length and feed conversion rate of shrimp species.

Giant freshwater prawn (Macrobrachium rosenbergii). Growth and survival of giant freshwater prawn was enhanced when prawns were fed *Bacillus* sp., isolated from the same animal species; either orally or as an immersion route (Rahiman et al., 2010). In addition, an improvement in some immune variables; total hemocyte count, phenoloxidase and respiratory burst activities of giant freshwater prawn, suggesting probiotic species-specific effect in this prawn species.

Kuruma shrimp (Marsupenaeus japonicus). Dong et al. (2014) evaluated the role of *Bacillus* as protective agent and immunomodulator in kuruma shrimp juveniles against temperature stress. The study revealed that *Bacillus* improved growth, minimized damage caused by free

radicals generated from insufficient oxygen metabolism and enhanced the immune response of kuruma shrimp during the high temperature farming period.

Chinese white shrimp (Fenneropenaeus chinensis). Chai et al. (2016) showed that a *Bacillus* probiotic strain PC465, isolated from the gut of *Chinese white shrimp*, enhanced immune parameters including ProPO, peroxinectin, penaeidin, thioredoxin, lectins, haemocyanin and crustin, and provided protection against white spot syndrome virus infection in Pacific white shrimp.

Mud crab (Scylla paramamosain). In mud crab, dietary administration of *Bacillus* spp. isolated from the crab's intestine significantly enhanced survival rate, respiratory burst activity, immune related genes expression, and resistance to *Vibrio parahaemolyticus* (Wu et al., 2014).

Pacific oyster (Crassostrea gigas). A significant decrease in hemocytes mortality and increase resistance toward *V. harveyi* were observed in Pacific oyster fed a mixture of three *Bacillus* sp. isolated from Tunisian hypersaline (Fdhila et al., 2017).

5.2. Bacillus aquimaris

Ngo et al. (2016) selected eight pigmented *Bacillus* strains from Pacific white shrimp based on the production of heat-stable spores, carotenoids and their free-radical scavenging activity. One of these strains, *Bacillus aquimaris* SH6 a red-orange pigmented strain displayed the highest abundance in the gut of Pacific white shrimp, and by feeding Pacific white shrimp a diet containing SH6 spores at > 3 × 10^6 CFU g^{-1} for 4 weeks improved health benefits, coloration, growth and immunity were noticed. Compared with dietary astaxanthin administration, dietary SH6 spores are more beneficial for shrimp weight gain and immunity. Furthermore, as a 300-fold higher concentration of SH6 spores than conventional probiotic concentrations was not toxic to the shrimp, it was concluded that SH6 spores can be a potential supplement as a carotenoid-producing probiotic strain for Pacific white shrimp.

5.3. Bacillus aryabhattai

Tepaamorndech et al. (2019) demonstrated that the supplementation of *B. aryabhattai* to Pacific white shrimp reduced the abundance of *Vibrio* populations and modulated the bacterial community in the shrimp GI tract. Further, an enhancement in the innate immunity, antioxidant activity and disease resistance to *V. harveyi* was noticed, suggesting that *B. aryabhattai* isolated from shrimp environment (sediment) as a useful probiotic in shrimp aquaculture.

5.4. Bacillus cereus

To my knowledge, few studies have used *B. cereus* as probiotic in shrimp aquaculture. Bath administration of *B. cereus biovar toyoi* (10^5 CFU mL^{-1}) added daily, significantly decreased survival of giant tiger prawn in a larval-culture system (Guo et al., 2009). Yang et al. (2015) isolated 27 protease-producing bacterial strains from intestine of marine-growth Pacific white shrimp, among which a high-yield protease-producing strain, *B. cereus* was identified.

A number of studies have shown that species of *Bacillus* isolated from similar environment where they will be applied, can boost the cellular and humoral components of innate immunity in shrimp species. For example, *B. cereus* enhanced various immunological variables including phenoloxidase, lysozyme, respiratory burst, bactericidal activity in giant tiger prawn (Chandran et al., 2014). Furthermore, enhancement of immune status was confirmed by higher survival rates in treated shrimp after being challenged with *V. harveyi*. Later, Dou et al. (2016) isolated a *B. cereus* strain from Pacific white shrimp able to produce extracellular protease, amylase and lipase, and protected Pacific white shrimp against *Vibrio anguillarum* infection. In a recent study, Vidal, da Cruz Pessôa, dos Santos, Mendes, and Mendes (2018) revealed

that a *B. cereus* originally isolated from the intestine of juvenile Pacific white shrimp, and displayed that probiotic feeding significantly improved weight of Pacific white shrimp, but resistance against *V. parahaemolyticus* was not significantly improved. As the shrimp were only fed the probiotic bacteria for 7 days prior to bath challenge of the pathogen, one can speculate that the probiotic feeding time was too short, and this suggestion has to be confirmed in further studies.

5.5. Bacillus coagulans

Firstly, *B. coagulans* can promote intestinal digestion, as *B. coagulans* strains produce various enzymes that facilitate excretion and digestion. Secondly, *B. coagulans* can regulate host symbiotic microbiota and inhibit the growth of pathogenic bacteria. Lastly, due to its ability to normalize both the quantitative parameters of the immune system and immune cells' functional activity, *B. coagulans* can significantly benefit the host immune system. Due to the evidence supporting various probiotic effects of *B. coagulans*, many different strains of *B. coagulans* have been used in the management and alleviation of several human diseases. Therefore, direct supplementation or prebiotic modulation of *B. coagulans* may be an attractive preventive and/or therapeutic avenue for human diseases.

Several beneficial effects of *B. coagulans* have been reported, and due to its excellent stability, *B. coagulans* has been widely used in medicine, food and chemical industry. Recent studies have shown that *B. coagulans* has therapeutic effects on intestinal diseases, such as acute diarrhea, irritable bowel syndrome, antibiotic-related diarrhea, constipation and colitis via modulation of the microbiota composition, host immunity and metabolism (Mu & Cong, 2019). *B. coagulans* are known to improve digestive health by posing antagonistic effects on pathogens (Wang, Fu, & Lin, 2012). Additionally, toxicological experiments and a large number of clinical observations have showed that *B. coagulans* is safe, and has no effect of mutagenicity, teratogenicity or genotoxicity. *B. coagulans* at inclusion level of 10^7 CFU g^{-1} feed was administrated to Pacific white shrimp for 50 days (Wang et al., 2012). There appeared significant (P < 0.005) enhancement of final weight, daily weight gain, survival rate, and protease-, amylase- and lipase activities by probiotic feeding. However, no significant difference was noticed in muscle composition of moisture, crude protein and ash.

In the study of Zhou, Wang, and Li (2009), the effect of *B. coagulans* SC8168, as water additive was evaluated in larval Pacific white shrimp, and the results revealed that supplementation significantly increase survival rate and digestive enzyme activities (protease, amylase and lipase). In a recent study by Amoah et al. (2019), Pacific white shrimp were fed four different inclusion levels, 0, 10^6, 10^7 and 10^8 CFU g^{-1} of *B. coagulans* for 56 days. The results revealed that dietary supplementation modulate the gut microbiota as the abundance of opportunistic pathogenic bacteria such as *Vibrio*, *Tenacibaculum* and *Photobacterium* significantly decreased with increasing probiotic inclusion. Furthermore, probiotic supplementation significantly improved growth performance as well as immune- and antioxidant response [triglyceride, lysozyme, acid phosphatase, glutathione peroxidase, and malondialdehyde], digestive enzyme activities (lipase, amylase and trypsin), and intestinal morphology. In addition, a challenge test revealed enhanced resistance against *V. parahaemolyticus* at inclusion level of 10^8 CFU g^{-1}, and based on their results the authors concluded that *B. coagulans* at supplementation level of 10^8 CFU g^{-1}, is a promising probiotic in Pacific white shrimp culture.

5.6. Bacillus flexus

Cai et al. (2019) conducted a 30-day feeding trial and a subsequent challenge test using *V. harveyi* to determine the effects of *B. flexus*, isolated from pond water/sediment, and revealed enhanced growth performance, immune related enzymes (alkaline phosphatase, peroxidase and lysozyme), digestive enzymes (protease and lipase), stress

tolerance and disease resistance.

5.7. Bacillus fusiformis

Bath administration of *B. fusiformis* (10^5 CFU mL^{-1}) added either daily or every 2nd day, increased survival in the larval-culture system of Pacific white shrimp (Guo et al., 2009).

5.8. Bacillus licheniformis

B. licheniformis is another efficient *host-associated probiotic* in aquaculture. A strain of *B. licheniformis* with the ability to secrete extracellular macromolecule-digesting enzymes, isolated from the surface sediment of shrimp pond was added to shrimp tanks at concentrations of 10^3, 10^4 and 10^5 CFU mL^{-1} for 40 days (Li et al., 2007b).

Dietary *B. licheniformis* supplementation has revealed to improve resistance towards *V. harveyi* in Pacific white shrimp by inhibiting the growth of intestinal *Vibrio*, and increasing the expression of genes related to disease resistance (Zhang et al., 2016). Similar results were revealed by Cai et al. (2019) conducted a 30-day feeding trial and a subsequent challenge test using *V. harveyi* to determine the effects of *B. licheniformis flexus*, and revealed enhanced growth performance, immune related enzymes (alkaline phosphatase and lysozyme), digestive enzymes (protease and lipase), stress tolerance and disease resistance towards *V. harveyi*.

5.9. Bacillus pumilus

Bacillus pumilus is a *host-associated probiotic* of recently interest in aquaculture. Use of *B. pumilus* as a known nitrogen removal bacterium together with periphytic algae in a biofloc system; reduced total ammonia and nitrite as demonstrated elsewhere (Banerjee, Khatoon, Shariff, & Yusoff, 2010), where *B. pumilus* was added to the rearing water of giant tiger prawn. Furthermore, no significant change were revealed in pH, salinity, dissolved oxygen and temperature. *In vitro* bioremediation assessment of three indigenous *Bacillus* species; *B. pumilus*, *B. licheniformis* and *B. subtilis,* isolated from marine water and soil samples showed that these bacteria were able to reduce total ammonia nitrogen, in tank water of giant tiger prawn (Devaraja, Banerjee, Sariff, & Khatoon, 2013), and thus recommended *Bacillus* as a bioremediator for giant tiger prawn culture systems. *In situ* bioremediation has also been widely applied in aquaculture through bio-augmentation using indigenous or exogenous probiotics, which ameliorate water quality (Wang, Xu, & Xia, 2005). Based on their results by inclusion of *B. subtilis* at three doses, 10^6, 10^7 and 10^8 CFU g^{-1}, Zhao et al. (2019) revealed that administration of *B. pumilus* at dose of 10^8 CFU kg^{-1} improved growth, immunity and digestive enzyme activities of giant freshwater shrimps.

5.10. Bacillus stratosphericus

Dietary administration of *B. stratosphericus* to abalone (*Haliotis diversicolor*) for 180 days and challenged with *V. harveyi* (Zhao, Ling, Zhang, Ke, & Hong, 2018), revealed improved nutrient and health status, but no significant disease resistance was noticed towards *V. harveyi*.

5.11. Bacillus subtilis

B. subtilis is one of the most studied species within genus *Bacillus*. It has been also shown that *Bacillus* feeding increased the survival of shrimp species against bacterial and viral pathogens through immune modification. For example, bath treatment of giant tiger prawn with cell-free extracts of *B. subtilis* BT23 significantly reduced mortality level after shrimp being challenged with *V. harveyi* (Vaseeharan & Ramasamy, 2003), while Keysami, Saad, Sijam, Daud, and Alimon

(2007) studied by using *B. subtilis*, on larval growth and development rate of fresh water river prawn in Malaysian hatchery. *B. subtilis* E20, isolated from fermented soybeans, has been reported to improve the resistance of Pacific white shrimp exposed to *Vibrio alginolyticus* through stimulation of immune responses variables such as lysozyme and prophenoloxidase I and II, survival and stress tolerance to water temperature, salinity and nitrite-N in Pacific white shrimp (Liu, Banerjee, Sariff, & Khatoon, 2010). Liu, Chiu, Shiu, Cheng, and Liu (2010) supplemented Pacific white shrimp diets with two doses (10^8 CFU and 10^9 CFU L^{-1}) of different *B. subtilis* E20 for 14 days, and at the end of feeding trial shrimp were exposed to stress test; suddenly exposed to fresh water and 60‰ salt water. The results recorded that postlarvae had significantly lower cumulate mortality in the probiotic treatments. Analysis of immune-related gene expressions showed that the expression of prophenoloxidase I, prophenoloxidase II, and lysozyme of larvae significantly increased after being reared in probiotic-containing water. However, no significant difference in serine proteinase or glutathione peroxidase gene expressions was revealed. Based on their results, the authors suggested that 10^9 CFU L^{-1} of B. subtilis E20 should be added to the rearing water for shrimp larva breeding.

In a study by Olmos et al. (2011), improved growth performance and better stress tolerance to ammonia oxygen deficiency was revealed in juvenile Pacific white shrimp orally fed with *B. subtilis* compared to both control shrimps and those fed with *Bacillus megaterium*, suggesting that probiotic species selection is an important factor.

Zokaeifar et al. (2012; 2014) demonstrated that administration of *B. subtilis* at two different doses, 10^5 and 10^8 CFU g^{-1} fed to Pacific white shrimp increased the activity of protease and amylase digestive enzyme and subsequently improved the growth (final weight and weight gain) of shrimp juveniles. However, food conversion ratio (FCR) was unaffected by probiotic feeding. Expression of immune-related genes was significantly up-regulated. After eight weeks of probiotic feeding was shrimp challenged with *V. harveyi*, and the results revealed significant protection. Administration of *B. subtilis* fed at 5×10^9 CFU, 5×10^{10} CFU and 5×10^{11} CFU kg^{-1} to Pacific white shrimp for 8 weeks and challenged with *V. harveyi* (Liu et al., 2014). There was significant enhancement of phagocytic rate, lysozyme, superoxide dismutase phenoloxidase and antibacterial activity and disease resistance against *V. harveyi*, while body crude lipid decreased significantly. Application of an indigenous probiotic *B. subtilis* once a week into a Pacific white shrimp culture enhanced water quality by decreasing pH, nitrite, water transparency and soluble reactive phosphorus, and increasing COD and Chlorophyll a (Wu et al., 2016). Probiotic administration also affected the bacterial community of culture water, with greater impact in the early and middle phases, than in the late phase of shrimp culture. The greater impact early in culture can probably be attributed to faster initial colonization and multiplication of the probiotic through peptone addition in the water column. Recently, Interaminense et al. (2018) reported that *B. subtilis* administration enhanced Pacific white shrimp growth and reduced *Vibrio* counts in hepatopancreas. However, *Vibrio* counts in intestine and faeces increased during probiotic administration. This study also investigated the effect of probiotic feeding of *Shewanella algae*, and clearly revealed difference by the probiotic administrations.

5.12. Bacillus thuringiensis

Dou et al. (2016) isolated a *B. thuringiensis* strain from Pacific white shrimp able to produce extracellular protease, amylase and lipase, and protected Pacific white shrimp against *Vibrio anguillarum* infection.

5.13. Bacillus vireti

Hindu, Chandrasekaran, Mukherjee, and Thomas (2018) conducted a 2 week feeding trial of freshwater prawn and a subsequent 15 day infection trial to determine the effects of *B. vireti* on antioxidant defense

enzymes activities and disease resistance against *Pseudomonas aeruginosa*. The results revealed considerably higher antioxidant defense enzymes activities, superoxide dismutase, catalase and GSH in muscle, hepatopancreas and gills of prawns infected by the pathogen by probiotic administration, leading to improved resistance against *P. aeruginosa*.

5.14. Mixture of Bacillus

Use of a commercial probiotic product, Sanolife MIC, mixture of some bacilli strains; *B. subtilis* and *B. licheniformis*, administered in hatcheries of giant tiger prawn and Pacific white shrimp, improved water quality and reduced the density of *Vibrio* bacteria in the water column (Decamp, Moriarty, & Lavens, 2008). Other species within genus *Bacillus*; *Bacillus* OJ, *Bacillus amyloliquifaciens*, and *Bacillus aerophilus*, isolated from GI tracts of Pacific white shrimp, yellow fin bream (*Acanthopagrus latus*), and rohu significantly enhanced growth performance, immune response, and disease resistance of Pacific white shrimp (Li et al., 2009).

Rahiman et al. (2010) reported lower values of ammonia, nitrite and pH in giant fresh water prawn culture ponds treated with *Bacillus* sp. during 60 days cultivation, while no change was observed in dissolved oxygen compared to control ponds. Similarly, Lara-Anguiano et al. (2013) demonstrated that the use of molasses as a fertilizer increased *Bacillus* spp. density in the water column of Pacific white shrimp. Nimrat, Suksawat, Boonthai, and Vuthiphandchai (2012) revealed lower levels of pH, ammonia and nitrite in treated Pacific white shrimp ponds *vs.* controls, when two mixtures of *Bacillus* species (first mixture - *B. thuringiensis, B. megaterium, B. polymyxa, B. licheniformis, B. subtilis*, and second mixture - *B. subtilis, B. polymyxa, B. megaterium, B. circulans, B. pumilus)* were used in the form of microencapsulated probiotics. Zokaeifar et al. (2014) reported that application of a *Bacillus* spp. mixture into the culture water of Pacific white shrimp revealed significant improvement in water quality parameters (reduction in ammonia, nitrite and nitrate ions) and increased growth performance, digestive enzyme activity, immune response and disease resistance against *V. harveyi*. In other studies, administration of *Bacillus* spp. (e.g. *B. subtilis, B. licheniformis*) to Pacific white shrimp culture water, enhanced the activity of immune parameters including prophenoloxidase (ProPO), peroxinectin, lipopolysaccharide and β-1,3-glucan-binding protein, lysozyme and serine protein (Madani, Adorian, Ghafari Farsani, & Hoseinifar, 2018; Zokaeifar et al., 2014, 2012). Moreover, the probiotic bacteria also enhanced disease resistance in Pacific white shrimp juveniles against pathogenic *V. harveyi* (Zokaeifar et al., 2012, 2014). Recently, Cai et al. (2019) revealed enhanced weight gain and SGR of Pacific white shrimp and improved water quality, stimulated innate immune enzyme activities, digestive enzyme activities, stress tolerance and disease resistance to *V. harveyi* in shrimp after feeding *B. licheniformis* and *B. flexus* either in single or in a combined form for 21 days at 28 °C.

In most probiotic shellfish studies, evaluations have concentrated on the effect to promote the growth of cultures organisms, enhancement of the immune system and on control and outcompete the pathogens. However, less information is available on the probiotic effect on the gut microbiota. This is of importance to evaluate, as the gut microbiota provide multitude biological functions including growth, metabolisms, development and immunity. Vargas-Albores et al. (2017) evaluated the probiotic administration of *Bacillus* and Gamma-proteobacteria on the gut microbiota of Pacific white shellfish. Alpha diversity values (Shannon-index) were higher, 2.03 for shrimp reared in the probiotic-based system, compared to 1.64 for shrimp held in the traditional system. The taxonomic profile of the shrimp microbiome revealed that some bacteria were common, but probiotic administration had a significant effect on the bacterial profile, as bacteria belonging to Proteobacteria (*Methylomonas methanica*, *Pseudomonas stutzeri*, and *Pseudoxaanthomonas suwonensis*), Firmicutes (*B. subtilis* and *Geobacillus*

thermoleovorans), Bacteroides (*Sphingobacterium ingobacterium*), Deinococcus - Thermus (*Oceanithermus profundus*) and Tenericutes (*Mycoplasma synoviae*) were detected in shrimp cultured with the probiotic mixture.

5.15. *Bacillus and poly-β-hydroxybutyrate (PHB)*

In addition to the beneficial role of probiotics on shrimp growth, there are also reports suggesting that application of poly-β-hydroxybutyrate (PHB), a bacterial storage compound deposited intracellular in cytoplasm a cellular energy and carbon reserve by various bacterial species, have been reported as a biocontrol agent for crustacean culture and revealed promising control of vibriosis (Borah, Thakur, & Nigam, 2002; Defoirdt, Boon, N., Sorgeloos, Verstraete, & Bossier, 2007; Jiang et al., 2008; Sui, Cai, Sun, Wille, & Bossier, 2012). Two previous studies, displayed that different *Bacillus* species from different sources accumulated high amount of under optimized conditions (Kaynar & Beyatli, 2009; Singh, Patel, & Kalia, 2009). Defoirdt, Boon, Sorgeloos, Verstraete, and Bossier (2007) displayed *B. thuringiensis* carry PHB, stimulated both the specific and non-specific immune mechanism in aquatic animals. Laranja et al. (2014) highlighted the beneficial role of PHB-accumulating *Bacillus* spp. on immunity and survival of shrimp species against pathogenic microorganisms. In a later study by the same research group, Laranja et al. (2017) reported that *Artemia* larvae enriched with *Bacillus* sp. JL47 with PHB increased the relative expression of innate immune genes for ProPO, transglutaminase (Tgase) and heat shock protein 70 (Hsp70) after challenge with *V. campbellii*.

Information about the use of other probiotics, *Aeromonas*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Clostridium*, *Paenibacillus*, *Phaeobacter*, *Pseudoalteromonas*, *Pseudomonas*, *Rhodosporidium*, *Roseobacter*, *Streptomyces*, *Vibrio* and other potential probiotics used in shellfish aquaculture are presented in Table 3.

6. Aeromonas

Genus *Aeromonas* is Gram-negative, facultative anaerobic, rod-shaped bacteria, and are mainly associated with diseases. In shellfish aquaculture less information is available on *Aeromonas* as probiotics. However, in an early study, Gibson, Woodworth, and George (1998) tested the probiotic ability of *Aeromonas media* strain A199 revealing antagonistic activity against several pathogens at 10^4 CFU mL^{-1} for 5 days on Pacific oyster (*Crassostrea gigas*) challenged with *Vibrio tubiashii*, and revealed a significant effect on survival after 5 days.

7. Alteromonas

Genus *Alteromonas* belongs to family Alteromonadaceae is commonly isolated from sea water, either in the open ocean or in the coast. They are Gram-negative and are curved rods with a single polar flagellum. Some information is available on *Alteromonas* as probiotics in shellfish aquaculture. Douillet and Langdon (1994) revealed that strain CA2, probably an *Alteromonas*, enhanced survival and growth of Pacific oyster (*Crassostrea gigas*) when administered in water. In two studies testing potential probiotics, Kesarcodi, Miner, Nicolas and Robert (2010) revealed that *Alteromonas macleodii* 0444 controlled of *Vibrio splendidus* infection in Greenshell mussel (*Perna canaliculus*). Later, Kesarcodi, Kaspar, Lategan and Gibson (2012) displayed that strain 0444 also protected scallop (*Pecten maximus*) and flat oyster (*Ostrea edulis*) larvae against *V. coralliilyticus*, *V. splendidus* and *V. pectenicida* infections.

8. Arthrobacter

Arthrobacter, a genus of Gram-positive bacteria, have no spores and capsule, utilize a wide and diverse range of organic substances and displayed ability to produce antimicrobial compounds. Li et al. (2006)

revealed that *Arthrobacter* XE-7 isolated from the culture water of Chinese white shrimp (*Penaeus chinensis*) and supplemented at a dose of 10^6 CFU mL^{-1} to *P. chinensis* in a 14 days study, and reported that the bacterium is non-pathogenic to the shrimp larvae, and increased total numbers of culturable bacteria in water; mostly related to the probiotic supplementation. In addition, NH$_3$–N and NO$_3$–N in the culture water was reduced. With regard to survival, administration did not affect survival. A 63-d feeding experiment determined the effects of dietary administration of *Arthrobacter* XE-7 on immune responses and resistance against *V. parahaemolyticus* in the Pacific white shrimp (Li et al., 2008). Probiotic supplementation increased total hemocyte counts, percentage phagocytosis, respiratory burst activity, and serum phenoloxidase activity. With increasing dietary supplementation of *Arthrobacter* XE-7, shrimp mortality decreased in the challenge study. *Vibrio* counts in intestine of shrimp fed the probiotic bacterium was generally lower than that in the control shrimp. Xia, Zhu, and Zhang (2014) conducted a 25-day feeding trial using *Arthrobacter* sp. CW9 isolated from guts of Pacific white shrimp, and revealed significantly higher survival rates, mean shrimp weights, phenoloxidase activity, phagocytic activity and clearance efficiency of Pacific white shrimp compared to control shrimp. Xue, Liang, He, and Wen (2016) reported significant improved survival of Pacific white shrimp administrated with *Arthrobacter enclensis* isolated from the water column of Pacific white shrimp at a dose of 10^9 CFU g^{-1} in a 4 day study. In order to fully to conclude the probiotic effect of *A. enclensis*; the study should lasted more than 4 days, and should evaluated immunostimulatory properties and challenge study.

9. Bifidobacterium

Bifidobacterium, called the "*good bacteria*", is the first bacteria to colonize the intestinal tract in infants as they pass through the birth canal. A number of health benefits have been claimed for probiotic bacteria such as *Bifidobacterium* spp. because of the potential health benefits. Bifidobacteria are not as acid tolerant as *Lb. acidophilus*; the growth of the latter organisms ceases below 4.0, while the growth of the *Bifidobacterium* spp. is retarded below pH 5.0 (Shah, 1997). However, these organisms are less incorporated into diets or rearing water in finfish and shellfish aquaculture. In a 95 days study, peptidoglycan (PG) derived from *Bifidobacterium thermophilum* enhanced the phagocytic activity of granulocytes and increased resistance of *P. japonicus* when challenging to *Vibrio penaeicida* (Itami et al., 1998), but PG administration had no effect on body weight.

10. Clostridium butyricum

C. butyricum commonly reported in soil and intestines of healthy animals and humans is a butyric-acid producer and Gram-positive bacterium, and some strains have been used as probiotics to enhance growth and immune response in animals, humans as well as finfish (e.g. Han et al., 1984; Kuroiwa, Kobari, & Iwanaga, 1990; Nayak, 2010; Pan et al., 2008). In shellfish aquaculture some information exists on the use of *C. butyricum* as probiotics. Duan et al. (2017) conducted a 56-day feeding trial to determine the effects of *C. butyricum* on growth performance, health status, and resistance to ammonia stress in Pacific white shrimp, revealed increased growth performance, intestinal amylase and protease activity in the C. butyricum groups, while lipase activity was only affected in two groups. Total antioxidant capacity content, lysozyme activity, and the relative expression level of Toll and immune deficiency gene increased in probiotic groups. After exposion of ammonia stress, intestine immune biochemical parameters and genes (HSP70, Toll and Imd) expression level increased by C. butyricum feeding. Furthermore, probiotic administration increased the intestine epithelium height. Li, Tian, and Dong (2019a) fed *C. butyricum*, inclusion levels of 10^7–10^{12} CFU kg^{-1}, to Pacific white shrimp for 42 days and challenged with *V. parahaemolyticus*. There was significant

enhancement of specific growth rate, feed conversion ratio, intestinal villi height and intestinal wall thickness. Activities of alkaline phosphatase, acid phosphatase, lysozyme and total nitric oxide synthase in serum. However, probiotic administration did not affect superoxide dismutase activity. Respiratory burst activity of haemolymph was significantly higher at administration of 10^8–10^{12} CFU kg^{-1}. Moreover, inclusion of 10^{11} and 10^{12} CFU kg^{-1} revealed significant higher survival when Pacific white shrimp were challenged with *V. parahaemolyticus*. Li, Tian, Zhao, Jiang, and Dong (2019b) revealed that *C. butyricum* increased growth performance, improved intestinal histology in mid intestine, immune gene expression, and disease resistance against *V. parahaemolyticus*.

11. Neptunomonas

Genus *Neptunomonas* belong to family Oceanospirillaceae (Garrity, Bell, & Lilburn, 2005) within *Gammaproteobacteria*, and are Gram-negative, facultative aerobic, oxidase and catalase positive, and they can use several carbohydrates, sugar alcohols, organic acids, and some PAH as sole carbon and energy sources. Kesarcodi-Watson, Miner, Nicolas and Robert (2010) demonstrated that *Neptunomonas* 0536 was capable to control infection caused by *V. splendidus* in Greenshell mussel (*P. canaliculus*).

12. Paenibacillus

Previously, *Paenibacillus* species were included in genus *Bacillus* due to their common morphological and physiological characteristics with the type species *B. subtilis.* However, in 1993, *Paenibacillus* was reassigned as a new genus based on 16S rRNA gene sequences. Genus *Paenibacillus* has been isolated from humans, animals, and plants, but their use as probiotics in shellfish aquaculture is less investigated. Ravi, Musthafa, Jegathammbal, Kathiresan, and Pandian (2007) isolated *Paenibacillus* from marine sediment and reported antagonistic activities against *Vibrio* strains. Based on their results, the author used the *Paenibacillus* strain in a challenge study, and revealed improved disease resistance of giant tiger prawn against *V. harveyi*. This results was surprising as giant tiger prawn was only treated for probiotic administration for one day prior to challenge.

13. Phaeobacter

Phaeobacter belongs to the *Roseobacter* clade of α-Proteobacteria. *Phaeobacter gallaeciensis* improve the disease resistance of scallop larvae against *V. coralliilyticus* and *V. splendidus*, and also protected flat oyster larvae against *V. coralliilyticus* and *V. pectenicida*, and Pacific oyster larvae against *V. coralliilyticus*, but no protection was noticed against *V. pectenicida* (Kesarcodi-Watson, Kaspar, Lategan, & Gibson, 2012). *P. daeponensis* is seldom used as probiotic in shellfish aquaculture, but recently Zhao et al. (2018) conducted a 180-day feeding trial to determine the effects of *P. daeponensis* on growth and health status of abalone, and disease resistance against *V. harveyi*. The results revealed significant enhancement in shell length, wet weight, glutathione peroxidase-, catalase, alkaline phosphatase-, acid phosphatase- and superoxide dismutase activities, and disease resistance against *V. harveyi* and modulation of the gut microbiota.

14. Pseudoalteromonas

Genus *Pseudoalteromonas*, Gram-negative bacteria, previously members of genus *Alteromonas* is well-known to produce a wide variety of biologically active secondary metabolites (Bowman, 2007). In an early study, Longeon et al. (2004) isolated a *Pseudoalteromonas* sp. X153 with high similarity to *Pseudoalteromonas piscicida* from marine environment and displayed that the crude culture was highly active against human pathogens as well as *Vibrio* strains. The probiotic strain

was further tested in a challenge experiment with scallop (*Pecten maximus*), and the results revealed improved disease resistance against *Vibrio* sp. *Pseudoalteromonas* CDM8 and CDA22 isolated from hindgut of Pacific white shrimp was fed to Pacific white shrimp for 28 days and challenged with *Vibrio parahaemolyticus* (Wang et al., 2018), and significant enhancement of disease resistance was noticed. Moreover, viable *Vibrio* counts in hindgut was revealed. Sorieul et al. (2018) revealed that *Pseudoalteromonas* sp. NC201 isolated from marine environment, enhanced survival by hyposaline stress of Pacific shrimp, and disease resistance against *V. nigripulchritudo*, but the relative gene expression of lysozyme and penaeidin evaluated 24 h post infection was lower in probiotic fed shrimp.

15. Pseudomonas

Genus *Pseudomonas* is Gram-negative bacteria belonging to the family Pseudomonadaceae and containing nearly 200 species. The genus has a great metabolic diversity, inhibiting a wide range of pathogenic bacteria (Ninawe & Selvin, 2009), and are able to colonize a wide range of niches, including the GI tract of finfish and shellfish. Alvandi et al. (2004) isolated some Gram-negative bacteria (*Pseudomonas* sp. PM11 and *Vibrio fluvialis* PM17) from the gut of farm-reared shrimp, giant tiger prawn, and tested for their effect on the immunity indicators of black tiger shrimp. However, the results did not indicate desirable effect of improvement of the immune system in the shrimp. Administration of *Pseudomonas aestumarina* isolated from intestine of adult Pacific white shrimp was fed to Pacific white shrimp for 28 days and challenged with *V. parahaemolyticus* (Balcázar, Rojas-Luna, & Cunningham, 2007), and revealed significant enhancement of final weight, FCR and disease resistance against *V. parahaemolyticus*. The application of *Pseudomonas* probiotics (*P. synxantha* and *P. aeruginosa*) improved FCR of Western king prawn (*Penaeus latisulcatus*), but no difference was revealed in SGR and survival (van Hai, Buller, & Fotedar, 2009b), but administration of probiotics, enhanced the number of probiotics in intestine of prawn and lower the bacteria numbers in haemolymph.

16. Rhodosporidium

Genus *Rhodosporidium*, yeast cells are globose, ovoid, or elongate and budding is multilateral or polar. The genus form visible carotenoid pigments and the cultures are pink to orange in color. In sexual reproduction it is seen that some species are heterothallic, whereas others are self-fertile (Sampaio, 2011, pp. 1523–1539). According to Scholz et al. (1999), *Rhodosporidium* a carotenoid-rich red yeast, has successfully been used as dietary supplement in aquaculture as it reduces oxidative stress in aquatic animals. A strain of *R. paludigenum* obtained from the coastal water at Zhanjiang, China has been included in the diet of Pacific white shrimp due to its high carotenoid content and because the strain exhibits safe and nontoxic growth in the intestinal mucus (Yang, Wu, Jian, & Zhang, 2010). Dietary administration of either live (10^8 CFU/g diet) or dry *R. paludigenum* (1 g/100 g diet) for 42 days to the shrimp significantly increased growth, serum and total antioxidant competence in muscle, and hepatopancreatic superoxide dismutase and glutathione peroxidase activities and decreased the malondialdehyde content in muscle. Dietary dry *R. paludigenum* significantly increased hepatopancreatic protease and lipase activity in shrimp, in contrast to live *R. paludigenum* which only increased protease activity. Both live and dry *R. paludigenum* administration to the diet of shrimp decreased the total *Vibrio* count in the intestine.

17. Roseobacter

Roseobacters, first described in 1991 with the discovery of *Resobacter litoralis* and *Roseobacter denitrificans*, and both were pink-pigmented bacterialchlorophyll strains isolated from marine algae. *Roseobacter* are thought to promote algal growth by biosynthesizing and

secreting antibiotics and growth stimulants (auxins). Ruiz-Ponte, Samain, Sanchez, and Nicolas (1999) isolated a *Roseobacter* (BS 107) from marine environment and revealed that the bacterium in co-culture with *V. anguillarum*, was inhibitory to *Vibrio*, with cell extracts of BS107 enhancing the survival of larval scallop (*Pecten maximus*). Balcázar et al. (2007) revealed significant improvement of survival, final weight, FCR and disease resistance against *V. parahaemolyticus* in study where *Roseobacter gallaeciensis* isolated from intestine of adult Pacific white shrimp was fed to Pacific white shrimp for 28 days and challenged with *V. parahaemolyticus*.

18. Streptomyces

Genus *Streptomyces* (phylum: *Actinobacteria*) are Gram-positive, high G + C (70%) genome content, soil-living bacteria with characterized branching filamentous morphology, and is an excellent antibiotic producer (Tan, Chan, Lee, & Goh, 2016; Tarazona, León, Galindo, Vallejo, & Marguet, 2018), and produce extract inhibits biofilm formation (Balasubramanian et al., 2017). The probiotic effects by *Streptomyces* through different mechanism of actions are; antagonistic compound production, anti-biofilm and anti-quorum sensing activity, anti-virulence activity, anti-viral activity, exoenzymes secretion, low pH tolerance and intestinal enzymes resistance etc. (Tan et al., 2016). The potential of *Streptomyces* as probiotics in aquaculture has recently been reviewed by Tan et al. (2016), but is to a lesser extent used in shellfish aquaculture (Das, Lyla, & Khan, 2006, 2010; Aftabuddin, Kashem, Kader, Sikder, & Hakim, 2013; Augustine, Jacob, & Philip, 2016; García Bernal et al., 2018; García Bernal, Medina Marrero, Campa-Córdova, & Mazón-Suástegui, 2017; Liu et al., 2014).

In an early study, *Streptomyces* was used as a probiotic in a laboratory culture of giant tiger prawn, and the results revealed better water quality parameters, increased length and weight in terms of growth *vs.* control fed shrimp (Das, Lyla, & Khan, 2006). Later, the same research group (Das, Ward, & Burke, 2010) displayed that feed supplemented with *Streptomyces* strain CLS-39 increased weight of giant tiger prawn, and the authors suggested that *Streptomyces* secreted hydrolytic exoenzymes which improved the amylolytic and proteolytic activity in the shrimp GI tract for more efficient use of the feed. The study further evaluated the efficacy of *Streptomyces* to protect the shrimp to *V. harveyi* challenge. Feed supplemented with *Streptomyces* sp. for 15 days revealed protection of giant tiger prawn in a 12 h challenge with *V. harveyi* (LD50 at $10^{6.5}$ CFU mL^{-1}).

Aftabuddin et al. (2013) isolated a *Streptomyces fradiae* from mangrove sediment; used the isolate in a study with giant tiger prawn, and revealed that inoculation of *S. fradiae* to the rearing water at a concentration of 10^6 bacteria mL^{-1} rearing water, and 10^9 bacteria g^{-1} feed; decreased CFU and viable *Vibrio* counts per mL rearing water. Furthermore, an improved growth performance was noticed, but best effect was revealed by dietary supplementation. It is also worth to mention that similar effects were noticed when B. megaterium was used. These results showed the probiotic potential of *Streptomyces*, but further evaluations including challenge - and immune response studies merits investigations.

Augustine et al. (2016) reported that a marine *Streptomyces rubrolavendulae* revealed antagonistic activity towards *V. harveyi, V. alginolyticus, V. parahaemolyticus* and *V. fluvialis* in an *in vitro* co-culture experiment. In order to confirm the *in vitro* findings, the authors displayed in a 28 day study that biogranules *S. rubrolavendulae* M56 resulted in improved survival of giant tiger prawn post-larvae with a reduction of viable *Vibrio* sp. in the culture system.

In a study with Pacific white shrimp, García Bernal et al. (2017) studied the effect of two Streptomyces strains, N7 and RL8, supplemented either alone or in combination with Bacillus and Lactobacillus for 30 days and challenged with V. parahaemolyticus. The results revealed no significant effect on growth performance by N7 and RL8 administration. The Streptomyces groups, displayed a significant

reduction of Vibrio from hepatopancreas, and the probiotic-fed groups had a higher hemocyte count. The challenge test revealed significantly higher survival rate by RL8 administration, but not by N7. Based on their results, the authors suggested that combination of *Streptomyces* and a *Bacillus* mixture, consisting of *B. tequilensis*, *B. endophyticus* C2-2 and *B. endophyticus* YC3–B2 was the most promising group by improving growth performance, immune response, modulating microbiota and enhanced resistance against V. parahaemolyticus. The same research group, García Bernal et al. (2018) highlighted the potential of Streptomyces strain N7 and RL8 by growth- and histological evaluations of hepatopancreas, and protection against V. parahaemolyticus of Pacific white shrimp.

Even though Tan et al. (2016) discussed limitations of *Streptomyces* as probiotics in aquaculture due to the two common semivolatile terpenoid compounds, geosmin and 2-methylisoborneol, the genus seems to have a probiotic potential that merits further investigations.

19. Vibrio

Genus *Vibrio* is Gram-negative, with a curved-rod (comma) shape and several species cause fish diseases. They are typically found in salt water, and they are facultative anaerobe and oxidase positive. Vibriosis is among the most common diseases leading to massive mortality of cultured shrimp, fish, and shellfish (Frans et al., 2011; Ina-Salwany et al., 2019). Even through most Vibrios caused diseases, some studies have used Vibrios as probiotic in finfish and shellfish aquaculture. A probiotic administration of *V. alginolyticus* original isolated from intestine of adult Pacific white shrimp was fed to Pacific white shrimp for 28 days and challenged with *V. parahaemolyticus* (Balcázar et al., 2007). There was significant (P < 0.001) enhancement of final weight, FCR and disease resistance against *V. parahaemolyticus*.

Dietary *Vibrio* NE17 was fed to giant fresh water river prawn for 60 days (Rahiman et al., 2010). There was significant enhancement of SGR, weight gain, survival, water quality parameters, total haemocyte counts, phenoloxidase and respiratory burst.

20. Other potential probiotics

Two studies have revealed enhanced disease resistance against *V. tubiashii* and *V. coralliilyticus* when *Phaeobacter* sp. S4 and *Phaeobacter inhibens* was administrated to Eastern oyster (*Crassostrea virginica*) and bay scallop (*Argopecten irradians*) by Karim, Zhao, Rowley, Nelson, and Gomez-Chiarri (2013) and Sohn et al. (2016), respectively. Xue et al. (2016) isolated 27 bacteria species from the water column of Pacific white shrimp and tested them by probiotic administration on survival of Pacific white shrimp. Of the tested bacteria, three strains, *Phaeobacter gallaeciensis*, *Arthrobacter enclensis* and *Microbacterium aquimaris* significantly enhanced survival of the shrimp. The reason for this may be due to antagonistic activity, degradation of toxic organic compounds and production of bioactive compounds, but this hypothesis merits further investigations.

21. Combination of several potential probiotics

Information on the use of commercial probiotics in shellfish aquaculture is available (de Paiva Maia, Alves-Modesto, Otavio-Brito, Olivera, & Vasconcelos-Gesteira, 2013; Kesselring et al., 2019; Madani, Adorian, Ghafari Farsani, & Hoseinifar, 2018; Nimrat et al., 2012; Porubcan, 1991; Wang et al., 2005). Some probiotic products like Super-biotic, Super Ps, Zymetin, and Mutagen (Soundarapandian, Ramanan, & Dinakaran, 2010) were reported to play a vital role in giant tiger prawn post-larvae by maintaining good water quality parameters throughout the culture period. Boonthai et al. (2011) fed a mixture consisting of *B. subtilis*, *B. megaterium* and *B. thuringiensis*; live sprayed and freeze-dried to giant tiger prawn for 120 days. The *Bacillus* species were isolated from giant tiger prawn intestine and shrimp pond, and the

results revealed increased *Bacillus* counts in hepatopancreas and intestine by probiotic administration. However, culturable bacteria counts in hepatopancreas, intestine and cultured water were not affected. The decreased counts of *V. parahaemolyticus*, *V. alginolyticus*, *V. vulnificus* and *V. cholera*, and *A. hydrophila*, *Shewanella putrefaciens* and *Photobacterium damselae* observed in hepatopancreas and intestine by probiotic feeding, respectively, and might be due to the antagonistic effects and out competition of the pathogenic bacteria; adherence and colonization.

Nimrat et al. (2011) reported that Pacific white shrimp fed freeze-dried microencapsulated probiotics, five *Bacillus* strains (*B. thuringiensis*, *B. megaterium*, *B. polymyxa*, *B. licheniformis* and *B. subtilis*) and two yeast strains (*Debaryomyces hansenii* and *Rhodotorula*) isolated from a shrimp pond, presented significantly improved growth performance, and survival rate; as well as increasing the number of additional beneficial microbial probiotics in shrimp larvae and postlarvae as well as bacterial community in culture water.

A multiple probiotic administration of *Lb. plantarum*, *Lb. salivarius* and *Lb. rhamnosus* isolated from the gut of female *P. pelagius* was fed to *P. pelagius* for 14 days (Talpur et al., 2012). There was significant enhancement of growth and protease and amylase activities by multiple probiotics administration. Even though beneficial results were revealed, further studies on the effect on immune system and disease challenge should be evaluated.

de Paiva Maia et al. (2013) appraised the efficacy of commercial *Bacillus* spp. probiotics on bacterial population and phytoplankton concentration in intensive Pacific white shrimp culture with a recirculation system. Probiotics bacteria improved total heterotrophic bacteria count in the sediment and caused a marked increase in the concentration of Pyrrophyta algae, and an improvement in the water and sediment quality. In closed recirculation systems, aeration is important to provide sufficient dissolved oxygen in the production system to maintain probiotic efficiency.

Nimrat et al. (2012) and Madani, Adorian, Ghafari Farsani and Hoseinifar (2018) assessed the effect of commercial *Bacillus* probiotics on growth performance, bacterial number, feed efficiency and body composition during rearing of Pacific white shrimp, and both studies revealed that administration of probiotics significantly improved length and weight gain, SGR and FCR compared to controls.

A microbial agens product MA containing Bacillaceae, Lactobacillaceae, Leuconostocaceae, Enterococaceae and Streptococcaceae and Rhodobacteraceae was fed Pacific white shrimp for 21 days (Liu et al., 2018). The results showed that MA feeding modulated the shrimp intestinal community, the relative abundance of Actinobacteria, Gammaproteobacteria, Deltaproteobacteria and Planctomycetes. However, probiotic feeding did not improve growth and survival. Azad et al. (2019) investigated the effect of a commercial product containing (*B. mesentericus*, *C. butyricum* and *Ent. faecalis*) at 5 g kg^{-1} to giant fresh water river prawn for 60 days and challenged with *Vibrio* spp. and *Aeromonas* spp. The results revealed significantly enhancement of total haemocyte count in the haemolymphs, resistance against *Vibrio* spp. and *Aeromonas* spp. Furthermore, probiotic administration modulate the culturable bacteria in water and intestine, by increasing the beneficial bacteria and declining some harmful bacteria.

A multiple-strain probiotics consisting of Lb. pentosus BD6, Lac. fermentum LW2, B. subtilis E20, *Saccharomyces cerevisiae* P13 at inclusion level of 10^7, 10^8 and 10^9 CFU kg^{-1}diet was fed Pacific white shrimp for 56 days and challenged with V. parahaemolyticus (Wang et al., 2019). There was significant enhancement of growth and health status of shrimp fed the diets containing BD6 and E20 at 10^9 CFU kg^{-1}, in contrast to diets containing P13 and LW2. No significant difference in the carcass composition was revealed among the control and treatments. Moreover, in groups fed the probiotic mixture groups, increased phenoloxidase activity, respiratory bursts, and lysozyme activity of hemocytes were revealed, leading to higher survival after injection with the *V. alginolyticus*. Based on their results, the authors suggested that the probiotic mixture could adequately provide probiotic efficiency for Pacific white shrimp, and recommended a probiotic mixture diet containing 10^8 CFU kg^{-1} diet.

22. Conclusions

The importance of probiotic administration, their beneficial health effects has been discussed in several reviews, for example Falcinelli et al. (2018) discussed the effect of probiotic appetite control, glucose and lipid metabolisms. Even though there is numerous information available on the use of probiotics in aquaculture, there is no concrete evidence to conclude that probiotics are better than immunostimulants or vaccines, the beneficial effects upon the host and their environment ensure that probiotics will remain one of the most promising approaches used to control diseases and the subsequent environmental modifiers (Newaj-Fyzul & Austin, 2015). In shrimp aquaculture, manipulation of microbiota using probiotics have been shown to control or inhibit pathogenic bacteria, improve digestive enzyme activity and growth performance, and enhance immune responses of the host against pathogenic infection or physical stress.

The functionality of gut microbiota, depends on the ability of microorganisms to interact within the GI tract, which benefit the host through influence on inflammation, metabolism, immunity and even behavior (e.g. Neuman, Debelius, Knight, & Koren, 2015; Boulange, Neves, Chilloux, Nicholson, & Dumas, 2016; Ramírez & Romero, 2017). When discussing disease resistance, the importance of a stable microbiota is of importance. In a early study, Collins and Carter (1978) revealed that germfree animals are more susceptible to diseases compared to corresponding conventional animals with a "*complete gut microbiota*". Germfree mouse was killed with 10 cells of *Salmonella enteritidis* whereas 10^6 cells were needed to kill conventional mouse with a conventional gut microbiota. Based in this finding, it is crucial to increase our knowledge on probiotics adhering and colonizing the GI tract of shellfish, in the context of improved growth performance and health.

In the recent review of Van Doan et al. (2019a) devoted to "*host-associated probiotics*" in aquaculture, the authors revealed benefits of host-associated probiotics to include improved growth performance, feed value, enzymatic contribution to digestion, inhibit adherence, and colonization of pathogenic microorganisms in the GI tract, increase hematological parameters, and immune response. Probiotics should be of animal-species origin. This criterion is based on ecological reasons, and takes into consideration the original habitat of the selected bacteria; part of the indigenous gut microbiota. In an early study, Moriarty (1998) suggested that probiotic cultures could also originate from the general rearing environments; since *Bacillus* spp. generally dwell in the sediment from which shrimps feed. Many studies believe that these bacteria have a better chance of out-competing resident bacteria and establishing themselves at a numerically significant level in their new host (e.g. Rengpipat et al., 2003; Alvandi et al., 2004; studies listed in Tables 1–3). In addition, the existence of a dominant bacterial strain in high densities in culture water indicates its ability to grow successfully under the prevailing conditions, and one can expect that this strain will compete efficiently for nutrients with possible harmful strains (Verschuere et al., 2000). The alternative strategy, *host-associated probiotics* within shellfish aquaculture has gained attention as numerous studies showed in Tables 1–3, have used probiotics isolated from the host environment or the host, which fit into the definition given by Van Doan et al. (2019a); "*bacteria originally isolated from the rearing water or the GI tract of the host to improve growth and health of the host*". However, in shellfish aquaculture, *per se* it is not clear, whether host-associated probiotics are more effective than probiotics from other origins, and this merits further investigations.

In future studies on probiotics in shellfish aquaculture, bio-floc culture system using probiotics should be investigated on growth performance, immune response, gut microbiome and disease resistance as only some information is available on this topic (Banerjee et al., 2010;

Correa et al., 2018; Dash et al., 2018; Kim, Min, Kim, Koo, & Kang, 2015; van Doan et al., 2019b). In addition to probiotics may also paraprobiotics (cell wall components; Taverniti & Guglielmetti, 2011) serve as an alternative to the use of antibiotics in prevention and treatment of infections caused by pathogens. In this regard it is of interest to notice that both probiotics and paraprobiotics can bind directly pathogenic bacteria, which limits adherence and colonization of the pathogen to gut cells.

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