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Lactic Acid Bacteria in Shellfish: Possibilities and Challenges

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ABSTRACT

Several investigations have investigated the gut microbiota in shellfish species, but less information is available on the favourable gut bacteria colonising the GI tract, the lactic acid bacteria (LAB), and these studies have revealed the presence of *Carnobacterium*, *Enterococcus*, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Streptococcus*, *Vagococcus* and *Weissella*. Identification of LAB in shellfish digestive tract are equally distributed between culture methods and culture-independent techniques. In the majority of the studies, the LAB are identified from the whole intestine or intestinal contents, while less studies have evaluated the autochthonous LAB.

Some LAB isolated from shellfish are able to produce antibacterial substances towards different potential fish pathogenic bacteria. They also play an important role in improving the feed utilisation and act as effective growth promoters in shellfish, and increase diseases resistance of shellfish culture against infectious bacteria and virus. In addition, enhancement of rearing water quality and increase the resistance against stressful condition have been recorded in shellfish fed LAB diets.

LAB effects on the shellfish innate immune system are mostly studied in shrimp. In addition to LAB species studied in finfish or mammal systems, autochthonous strains of LAB are also used for studies. Generally, LAB-treated shellfish (crustaceans, mollusc, and Echinodermata)

significantly improve innate immune parameters and display an increased survival rate from pathogen infections. Some of the studies indicate that the treatment of LAB mixture shows better immunomodulatory effects than that of a single strain of LAB. Studies of the underlying mechanisms of shellfish innate immune regulation are required for the identification of species-specific probiotics and the correct assessment of immunological effects.
The present review paper focuses on recent findings in the field of isolation and detection of LAB in the GI tract of shellfish, some information on their presence in hepatopancreas and in muscle, their administration as probiotic, their mode of action, and their interaction with shellfish immune responses.

INTRODUCTION

Shellfish is important in aquaculture with high economic value on a global scale, and in recent years, the development of high-density zootechnology and recirculation shrimp farming systems have imposed enhanced stressors on shrimp. In this respect, evaluation of the gut microbiota is of importance, as the gut microbiota provide multitude biological functions including growth, metabolisms, development and immunity. Compared to endothermic animals, the gut microbiota of aquatic animals is less investigated, even though several comprehensive reviews and studies has been published during the last decade (e.g. Romero et al., 2014; Ringø et al., 2016; Egerton et al., 2018). Even though several investigations have evaluated the microbial community in the gastrointestinal (GI) tract of shellfish (e.g. Zhang et al., 2014; Qiao et al., 2017; Sun et al. 2018; Li et al., 2018a), the topic is in early stages, and merits investigations, especially the beneficial gut bacteria; lactic acid bacteria (LAB). The favourable properties of LAB, production of bacteriocins, hydrogen peroxide, short chain fatty acids (SCFAs), delivery system of nanobodies, and to prevent adherence and colonisation of pathogens in the GI tract have been discussed in several comprehensive reviews (e.g. De Vuyst and Leroy, 2007; Li et al., 2018b; Ringø et al., 2018; del Rio et al., 2019).
The first study on shrimp microbiota was investigated by Tysset et al. (1961) using culture-dependent agar plating techniques. Today it is generally accepted that one of the dominant phyla in the GI tract of shellfish is Firmicutes (e.g. Sha et al., 2016a; Lu et al., 2017; Cornejo-Granados et al., 2018; Li et al., 2018a; Gao et al., 2019a), but per se less investigations have accessed on LAB in the gut microbiota of shellfish. When discussing the importance of LAB in the GI tract of shellfish, it is important to evaluate the dietary effect, but few studies have investigated the dietary effect; for example the effect of dietary lipid and carbohydrate on the gut microbiota of shellfish (Wei et al., 2016; Zhang et al., 2014; Qiao et al., 2017; Sun et al., 2018, 2019; Panigrahi et al., 2019), but none of these studies revealed LAB in the GI tract.
Several reviews have reported that functional feed additives such as probiotics; derived from Greek and meaning *for life*, can improve growth performance, utilisation of dietary components, digestive functions, modulate the gut microbiota, enhance immunity and disease resistance of shellfish, and improve water quality (Farzanfar, 2006; Ninawe and Selvin, 2009; van Hai and Fotedar, 2010; Kumar et al., 2016; Hoseinifar et al., 2018, 2019; Li et al., 2018a). Among the probiotics used in shellfish aquaculture, LAB are one of the promising used, and the 2nd aim of the present review is to present an update on LAB as probiotics in shellfish aquaculture, and on LAB data not mention in the aforementioned reviews.

Innate immunity is the first line defence system against pathogens in both vertebrates and invertebrates. Innate immune cells recognize microbes via pattern recognition receptors, which leads to the induction of immune responses, and eventually eliminates pathogens. Innate

immune responses are directly dependant on the activated status of degradation enzymes, synthetic enzymes of reactive oxygen species, phagocytic cells, clotting proteins, and complement proteins (Tripp, 1974; Bayne, 1983; Gross et al., 1999; Sritunyalucksana et al., 2000; Kimbrell et al., 2001; Pasquier, 2001; Salzet, 2001; Tort et al., 2003; Beutler, 2004; Ausubel, 2005; Magnadottir et al., 2006; Vazquez et al., 2009; Harikrishnan et al., 2011; Ringø et al., 2012, 2018; Chiaramonte et al., 2015; Romo et al., 2015; Song et al., 2015; Sánchez-Salgado et al., 2017; Smith et al., 2018). Generally, LAB affect various species including shellfish by improving their immune status, which leads to a more robust protection against various pathogens (Ige, 2013; Maeda et al., 2014; Merrifield et al., 2014; Vasama et al., 2014; Sha et al., 2016b; Ringø et al., 2018). Additionally, LAB act as probiotics by demonstrating weight gain effects, modulating specific immune tone status, and inhibiting colonization of pathogens (Balcázar et al., 2006; Kim et al., 2013, 2016; Vasama et al., 2014; Yeh et al., 2014; Beck et al., 2015, 2016, 2017; Ringø et al., 2018).

As the GI tract of aquatic organisms is one of the most important interfaces with the environment exposed to potential pathogens, and the fact that the GI tract is one of the major infection route (Birkbeck and Ringø 2015; Bøgwald and Dalmo 2014); the first aim of the present study address to evaluate the presence of LAB in the GI tract of shellfish. Furthermore, as LAB has the potential as probiotics and influence gut health, the current review aimed to present an updated overview of recently published data on health benefits of LAB as probiotics, their effect on the immune system.

As the present review do not discuss the pathogenicity of LAB, we recommend that readers with interest on this topic and disease control in shrimp aquaculture to have a closer look at the recent reviews of Xiong (2018) and Flegel (2019).

LACTIC ACID BACTERIA (LAB) IN THE GASTROINTESTINAL (GI) TRACT OF SHELLFISH

The GI tract microbiota in shellfish is divided into; the GI lumen microbiota (the allochthonous), and those that adhere to the mucosal surface (the autochthonous microbiota). In most shellfish studies, showed in **Table 1**, have characterized combination of allochthonous and autochthonous gut microbiota, isolated from the whole intestine with content, while few studies have focus on the autochthonous gut microbiota, which may be of importance in specialized physiological functions and by prevention adherence and colonisation of pathogens in the GI tract.

According to Merrifield et al. (2014) members belonging to *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Enterococcus*, *Streptococcus*, *Carnobacterium*, *Pediococcus* and *Weissella* genera are indigenous species in shellfish. In order to avoid duplication with that presented by Merrifield *et al*. (2014), lactic acid bacteria (LAB) isolated from the GI tract of Chinese shrimp (*Fenneropenaeus chinensis*), European lobster (*Homarus gammarus*), mud crab (*Scylla paramamosain*), swimming crab (*Callinectes* sp.), blue swimming crab (*Portunus pelagicus*), abalone (*Haliotis asinina*), oyster (*Crassostrea corteziensis*) and giant lion`s paw scallop (*Nodipecten subnodosus*) are not thoroughly discussed, only briefly presented. This subsection present investigations published post 2014 and papers not presented in the aforementioned review. Readers with special interest in studies only briefly presented in the text and in **Table 1** are recommend to have a closer look at the review of Merrifield et al. (2014) or the original papers.

Even though there is a paucity of studies which have investigated the indigenous gut bacteria in shellfish species compared to finfish, LAB have been reported in the GI tract of several shellfish species including shrimp, prawns, swimming crab (*Callinectes* and *Portunus* spp.) mud crab (*Scylla paramamosain*), scallop and abalone (**Table 1**).
The first study revealing LAB in the intestine of shellfish were displayed in giant freshwater shrimp (*Macrobrachium rosenbergii*) by Cai et al. (1999), where three isolates were identified to species level; *Lactococcus garvieae*, *Pediococcus acidilactici* and *Enterococcus faecium* by 16S rRNA gene sequencing.

Shrimp

In a study focus on exopolysaccharides (EPSs), long-chain polysaccharides, secreted by marine bacteria, Hongpattarakere et al. (2012) reported that *Lactobacillus plantarum* isolated from shrimp gut microbiota revealed high production of EPSs. Recently, Zhou et al. (2019) reviewed exopolysaccharides of LAB, and revealed that EPSs are widely produced by LAB. The importance to isolate EPSs producing bacteria are; EPSs are suggested to play a protective role against, desiccation, toxic compounds, bacteriophages, osmotic stress, and to permit adhesion to solid surfaces and biofilm formation (De Vuyst and Degeest, 1999).

Giant freshwater prawn (*Macrobrachium rosenbergii*)

The first study reporting LAB in the GI tract of giant freshwater shrimp was carried out by Cai et al. (1999). Later, Lalitha and Surendran (2004) reported that *Enterococcus* spp. accounted for 8.3% of the identified gut bacteria in adult giant freshwater shrimp, while Kennedy et al. (2006) revealed a smaller proportion, 4.5% of the culturable microbiota belonged to genus *Lactobacillus* in larval gut. In a probiotic study of giant freshwater shrimp, *Lb. plantarum* obtained from the culture collection of Chandigarh, India was used as probiotics (Dash et al., 2014, 2016), but in control fed prawn, only a small proportion (1.19 CFU g^{-1} intestinal tissue) of *Lactobacillus* sp. was displayed, *vs.* total viable counts; 6.84 CFU g^{-1} intestinal tissue.

Oriental river prawn (*Macrobrachium nipponense*)

Tzeng et al. (2015) investigated the bacterial community in the gut of oriental river prawn, and revealed that sequences assigned to genus *Lactobacillus* were frequently (1.2-8.9 %) in all six libraries investigated, while sequences assigned to *Streptococcus* were low (0.02-0.38%) in the libraries. In addition, *Leuconostoc* sp. was frequently revealed. Chen et al. (2017a) investigated the gut microbiomes using 16S rRNA amplicon sequencing on the Illumina MiSeq platform and revealed Latobacillales and Enterococcaceae. More recently, Zhao et al. (2018) explored the diversity and abundance of LAB in gut contents, allochthonous LAB, in oriental river prawn, and displayed that LAB constituted up to approximately 56.5 %, and belonged to Streptococcaceae (4.64 ± 1.32 %), Carnobacteriaceae (3.62 ± 0.98 %), Aerococcaceae (0.14 ± 0.83 %), Lactobacillaceae (0.01 ± 1.15 %), Enterococaceae (0.10 ± 0.93 %), and Leuconostocaceae (0.01 ± 0.13 %). Among the genera, were *Lactobacillus* and *Lactococcus* reported as the major LAB in the shrimp intestine. When the authors compared the LAB community in the GI tract of different shrimp species, they suggested higher abundance of LAB in freshwater shrimp *vs.* seawater shrimp. This notification is of importance, and merits further investigations.

Pacific white shrimp (*Litopenaeus vannamei*)

Pacific white shrimp is an important aquaculture species with a high economic value on a global scale, and is the most investigated shellfish species with regard to LAB in the GI tract. In an

early study, Vieira et al. (2007) isolated two LAB strains from the GI tract of juvenile Pacific white shrimp, and one of the strains later identified as *Lb. plantarum*, was used as probiotics (Vieira et al., 2008). In this study, total LAB counts in the intestine were low and not significantly different from control shrimps.

A previous study analyzing the bacterial community of Pacific white shrimp GI tract, revealed low population levels of *Lactobacillus* spp. and *Streptococcus faecalis* of both control and short-chain fructooligosaccharides (scFOS) fed shrimp (Zhou et al., 2007). Later. Vieira et al. (2010) identified LAB in the digestive tract of Pacific white shrimp, while Kosin and Rakshit (2010) identified *Lb. plantarum* and *Leuconostoc mesenteroides* subsp. *mesenteroides*/ *dextranicum* as autochthonous in the GI tract of Pacific white shrimp.

In the study of Kongnum and Hongpattarakere (2012), *Lb. plantarum* isolated from the intestinal tract of shrimp, species not specified, was used in a probiotic study, and cultivation analysis of the intestinal tract of Pacific white shrimp revealed LAB; coccoid shape and accounted for approximately 79 % of total LAB isolated.

It is generally accepted that one of the most promising gut bacteria, is genus *Bifidobacterium* (Gibson et al., 2017). Boonanuntanasarn et al. (2016) investigated the gut microbiota of dietary supplementation of β-glucan and microencapsulated probiotics (*Bacillus subtilis* and *Pediococcus acidilactici*) in *L. vannamei*, and detected LAB and *Bifidobacterium* sp. by cultivation. Genus *Bifidobacterium* is seldom isolated from shellfish intestine, and the study of Boonanuntanasarn and co-authors was the first one isolating *Bifidobacterium* sp. in shellfish, and revealed approximately log 5.6 CFU g^{-1} intestine in the control fed group, but the population level did not varied by dietary treatment. Huang et al. (2016) analyzed the intestinal bacterial community at four stages, 14 days postlarvae and 1-, 2- and 3-months old Pacific white shrimp and reported Lactobacillaceae in 1 month old juvenile and Streptococcaceae in 3 month old juvenile by 454 pyrosequencing techniques. LAB was not detected in the other stages.

In a probiotic study with Pacific white shrimp, *Lactobacillus* and *Enterococcus* were not detected in the intestine, even though *Lactobacillus pentosus* and *E. faecium* were supplemented (Sha et al., 2016c). The authors suggested that this observation may be due to low abundance; too low to be detected or to low adhesion ability. The latter suggestion is possibly true, as the probiotic bacteria used were originally isolated from the gut of Hazekuchi (*Acanthogobius hasta*), and not from Pacific white shrimp. To confirm this suggestion further studies are needed. When discussing the adhesion ability, it is of importance to remember that the adhesion ability to mucin can greatly varied among *Lb. plantarum* depending on their isolation habitats (Buntin et al., 2017).

In two studies, Adel et al. (2017a, 2017b) reported LAB in *L. vannamei* intestine. In a probiotic study using *Pediococcus pentosaceus*, previously isolated from healthy Pacific white shrimp intestine, Adel et al. (2017a) revealed $0.87 \pm 0.16 \times 10^5$ CFU g^{-1} intestine of *Lactobacillus* spp. in the control group, while $1.76 \pm 0.32 \times 10^5$ CFU g^{-1} intestine was detected in shrimp fed 10^8 *P. pentosaceus*. These population levels are lower compared to the dominant one; *Vibrio* sp., $12.16 \pm 1.63 \times 10^5$ CFU g^{-1} intestine in the control group, and $11.58 \pm 1.4 \times 10^5$ CFU g^{-1} intestine of *Micrococcus* spp. by feeding *L. vannamei* 10^6 *P. pentosaceus*. Adel et al. (2017b) identified a *Lactococcus lactis* subsp. *lactis* by biochemical analysis and 16S rRNA from intestine of *L. vannamei*, later used in a probiotic study. In the control group, not fed probiotics, the authors identified only a small proportion of *Lactobacillus*, 0.84 ± 0.13 CFU g^{-1} intestine.

In a study evaluating the intestinal microbiome in a Pacific white shrimp grow-out pond with possible outbreak of acute hepatopancreatic necrosis disease, Chen et al. (2017b) revealed 11 order taxa of which one was Latobacillales (*Weissella*).

The study of Cornejo-Granados et al. (2017) was the 2nd study isolating *Bifidobacterium* from intestine of shellfish; healthy Pacific white shrimp, unique for cultured samples.
In a probiotic study, Duan et al. (2017) used *Clostridium butyricum* and revealed that probiotic supplementation enriched *Lactobacillus* sp. and *Lactococcus* sp. in the intestine of Pacific white shrimp. The authors put forward the controversial hypothesis that enrichment of Firmicutes, including LAB, might contribute to the expression of host digestive – and immune-related genes, but to fully conclude, further studies are needed. In an eight-week feeding trial, He et al. (2017) evaluated the gut bacterial community of Pacific white shrimp fed AviPlus® (AP), a blend of organic acids [citric acid, 25%; sorbic acid, 16.7%, and essential oils (thymol, 1.7%; vanillin, 1.0%)], and revealed that dietary inclusion of 1.2 g kg^{-1} AP led to a significant increase in the abundance of *Lactobacillus* in shrimp gut *vs*. control. In a study evaluating sulfide exposure on gut health and gut microbiota of Pacific white shrimp, Suo et al. (2017) reported genera belonging to *Carnobacterium*, *Lactococcus*, *Lactobacillus*, *Leuconostoc*, and *Streptococcus* in the GI tract. Generally, the relative abundance of the LAB strains were higher in the control group *vs*. group exposed to sulfide. It is also worth mention, that the relative abundance of *Lactococcus* was highest among the major bacteria in both treatment groups. Among the 26 families detected from the intestine of Pacific white shrimp, Lactobacillaceae was revealed (Xiong et al., 2017), but only a small indicator value (0.54) was noticed as Lactobacillaceae was only detected in the retarded and normal groups. Zeng et al. (2017) identified *Lactobacillus* sp. from the microbiota of the Pacific white shrimp intestine, but the abundance was low, 0.04 %, compared to the dominant taxa, *Candidatus_Xiphinematobacter* (3.4 %) and *Propionigenium* (3.4 %). Zheng and Wang (2017) isolated 18 presumptive LAB strains, via culture-dependent techniques on MRS agar medium from GI tract of Pacific white shrimp, and tested them for extracellular protease, cellulase and lipase activities. One of the most promising isolate, strain AS13 was further identified by 16S rRNA gene sequence analysis and identified as *Lb. pentosus*, and further used in a probiotic study.
Chomwong et al. (2018) identified *Lb*. *plantarum* and *Lac*. *lactis* from the intestinal microbiota of the Pacific white shrimp in a study evaluating the LAB activating effect on the proPO system, and revealed that LAB increase resistance of an acute hepatopancreatic necrosis disease of *Vibrio parahaemolyticus*. Scanning electron microscopy analysis revealed adherence of the shrimp gut, and antibacterial activity against the Gram-positive bacteria, *Staphylococcus aureus*, *Aerococcus viridans*, *Bacillus megaterium* and *Bacillus subtilis*, and the Gram-negative bacteria, *V*. *parahaemolyticus*, *Vibrio harveyi* and *Escherichia coli*. A general finding was; *Lac*. *lactis* revealed higher antibacterial activities than *Lb*. *plantarum*.
Duan et al. (2018) explored the effect dietary poly-β-hydroxybutyrate (PHB) on the bacterial community of *L. vannamei*, and revealed that PHB increased the abundance of *Lactobacillus* sp. and *Lactococcus* sp., an effect that might improve shrimp intestinal health and disease resistance. In a comparative study analyzing the bacterial community in Pacific white shrimp intestine, rearing water and sediment, *Lactobacillus* sp. was one of the highly prevalent genus in the intestine (Hou et al., 2018). In addition, *Streptococcus* sp. was displayed. Synbiotic, combination of pro- and prebiotic, feeding using *Lb*. *plantarum* and galactooligosaccharide (GOS), revealed modulation of the microbiota in *L. vannamei* intestine; improved colonization of *Lb*. *plantarum* and reduced abundance of *Photobacterium damselae* and *V. harveyi* (Huynh et al., 2018).
In a probiotic study, Pinoargote et al. (2018) displayed relative low abundance of Lactobacillaceae in the gut when Pacific white shrimp were fed the control diets; 0.009 ± 0.003 and 0.006 ± 0.005 in negative and positive control, respectively. The families, Rhodobacteraceae, Vibrionaceae and Lactobacillaceae in the Pacific white shrimp gut varied

by supplementation of probiotics, but the relative abundance of Lactobacillaceae was significantly highest in shrimp fed *Lb. casei* or the commercial product, 0.089 ± 0.018 and 0.148 ± 0.027, respectively.

Xue et al. (2018) investigated the gut bacterial community in Pacific white shrimp gut at four larval stages, and revealed Leuconostocaceae and Streptococcaceae at stage Z2 (zoea 2) and M1 (mysis 1), but only Leuconostocaceae at stage P1 (postlarvae 1). It is worth mention, that Streptococcaceae was one of the most abundant groups at stage Z2 and M1. Fan et al. (2019) evaluated the gut bacterial community of Pacific white shrimp, and revealed genus *Lactobacillus* in shrimp gut. Gao et al. (2019b) reported genera *Lactobacillus* and *Streptococcus* in *L. vannamei* intestine; the highest abundance was noticed in postlarvae fed *Artemia* nauplii enriched with *Halomonas*-PHB particles. In a study evaluating biological water purification grid (BWPG) on bacterial community of Pacific white shrimp intestine, Pei et al. (2019) revealed that *Lactococcus* was enriched in the water of the test pond treated with BWPG, but the genus was not detected in the intestine; dominated by unclassified bacteria, which may indicate that the environmental *Lactococcus* was not able to colonise the intestine.

White shrimp (*Penaeus vannamei*)

By culture-dependent techniques, Kongnum and Hongpattarakere (2012) isolated *Lb. plantarum* MRO3.12 from the GI tract of white shrimp, and the strain possessed high antibacterial activity towards *V. harveyi*. In addition, co-cultivation of *Lb. plantarum* and *V. harveyi*, revealed complete reduction of the pathogen after 24 h, under aerobic and anaerobic conditions, in contrast to an increase of strain MR03.12 from log 5.3 to 9.5 CFU mL^{-1}. *Lb. plantarum* MRO3.12 was further used in a probiotic feeding trial with white shrimp. Sun et al. (2016) identified LAB from *P. vannamei* intestine, and these LAB were identified as *Lactococcus* sp. and *Lactobacillus* sp., but they accounted for a small proportion, 1.01 and 0.49 % of the intestinal bacterial community, respectively, compared to the dominant genus; *Pseudomonas*, 14.57 %. In a recent study, Gainza et al. (2018) explored the gut microbiota of *P. vannamei* in intensive ponds, harvest and nursery, and identified *Lac. garvieae* and *Lactococcus* sp. from harvest pond, while Lactobacillaceae was revealed in intestine of shrimp from the nursey pond.

Brown shrimp (*Farfantepenaeus californiensis*)

Only one study has revealed LAB in the intestine of brown shrimp (Leyva-Madrigal et al. 2011), and the authors addressed to isolate probiotic LAB to be used in Pacific white shrimp naturally infected with WSSV and IHHNV. Twenty presumptive LAB were isolated, and further analysis; haemolysis, growth, hydrophobicity, antibacterial activity against presumptive vibrios, and enzyme production revealed that the most promising isolates were identified as *P. pentosaceus*.

Indian white shrimp (*Penaeus indicus*)

Gopalakannan (2006) isolated 32 LAB, using culture-dependent methods, in the digestive tract of Indian white shrimp, and among them, LAB PI80 revealed high *in vitro* growth inhibition against *Aeromonas hydrophila*, and promising activity against *Aeromonas salmonicida*, *Vibrio anguillarum*, *Vibrio fischeri*, *Vibrio vulnificus* and *V. parahaemolyticus*. Kanmani et al. (2010) isolated *Streptococcus phocae* from the GI tract of Indian white shrimp, and tested the isolate for adherence, acid stability, antibiotic susceptibility, hemolytic properties and bacteriocins,

and was further used in a challenge study with *P. monodon* (Pattukumar et al., 2014). In a later study, the strain was tested for exopolysaccharide production and antibiofilm activity (Kanmani et al., 2011).

Kuruma shrimp (*Marsupenaeus japonicus*)

Maeda et al. (2014) isolated 51 LAB strains from the digestive tract of kuruma shrimp and identified them as *Enterococcus faecalis*, *Enterococcus*, *Enterococcus pseudovium*, *Enterococcus raffinosus*, *Lactobacillus* sp. *Lb. plantarum*, *Lactobacillus nagelii*, *Lac. garvieae*, *Lac. lactis*, *Pediococcus pentosaceus*, *Vagococcus campiphilus*, *Vagococcus* sp. and *Vc. fluvialis* by 16S ribosomal DNA sequencing. The 51 strains were tested for cellular immunomodulatory function by measuring the level of interferon (IFN)-γ induction in mouse spleen cell culture, and the most promising strain *Lac. lactis* D1813 was selected as probiotic in a *in vivo* study of kuruma shrimp.

Giant tiger prawn (*Penaeus monodon*)

In a previous study, Gopalakannan (2006) isolated 18 LAB, using culture-dependent methods, in the digestive tract of giant tiger prawn, but none of them displayed promising *in vitro* growth inhibition against *A. hydrophila*. Nimrat et al. (2013) isolated an *Enterococcus* sp. S2 from the intestine of giant tiger prawn and tested its hemolytic activity, *in vitro* growth inhibition towards *V. harveyi* and extracellular enzyme activity. Based on its promising properties, the strain was used in a probiotic study with giant tiger prawn. Rungrassamee et al. (2014) revealed *Lactobacillus* sp. and *Lactococcus* sp. in the GI tract of wild caught giant tiger prawn.

Yellow shrimp (*Metapenaeus brevicornis*)

Only one study have isolated and identified presumptive LAB strains, via culture-dependent techniques, in the GI tract of yellow shrimp (Kongnum and Hongpattarakere 2012). The isolates were further tested for antibacterial effects against *V. harveyi*, and the general finding was that the lactobacilli possessed the highest antibacterial activity.

Chinese shrimp (*Fenneropenaeus chinensis*)

The first study revealing LAB, *E. faecalis* in the GI tract of the Chinese shrimp was carried out by DGGE (Liu et al. (2011). In a later study, Sha et al. (2016b) displayed that presumptive LAB from the intestine of Chinese shrimp revealed probiotic potential in a study using Pacific white shrimp

Banana shrimp (*Fenneropenaeus merguiensis*)

In a culture-dependent study, Kongnum and Hongpattarakere (2012) isolated presumptive LAB in the GI tract of banana shrimp, but the strains were not further identified, and further use was not given.

European lobster (*Homarus gammarus*)

Two studies by Daniels et al. (2010, 2013) revealed *Weissella confusa* and *Weissella cibaria* in the GI tract of post-larval European lobster.

Narrow clawed crayfish (*Astacus leptodactylus*)

In a recent study, presumptive LAB was revealed in the intestine of narrow clawed crayfish fed diets supplemented 2 and 3 % GOS by cultivation (Nedaei et al., 2019). The population level of LAB after 97 days of feeding was log CFU g^{-1}, 4.52 ± 0.34 and 4.23 ± 0.26 by feeding 2 and

3 % GOS, respectively, but 14 days after switch to the basal diet, LAB counts was significantly reduced to approximately 2.6.

Mud crab (*Scylla paramamosain*)

A study assessing the GI tract of mud crabs identified *Weissella fabaria*, *Streptococcus mutans* and Latobacillales 1247 (Li et al., 2012).

Swimming crab (*Callinectes* sp.)

Uaboi-Egbenni et al. (2010) identified the well-known pathogen *Streptococcus agalactiae* in the GI tract of wild swimming crab.

Blue swimming crab (*Portunus pelagicus*) and swimming crab (*Portunus trituberculatus*)

One previous study reported LAB in the GI tract of blue swimming carp (Talpur et al., 2012). More recently, Kim et al. (2017) evaluated the intestinal microbial community in wild caught swimming crab in spring and autumn, and revealed higher microbial diversity in autumn than in spring. The dominant genera in spring were, *Psychrobacter*, *Vagococcus*, *Carnobacterium*, *Lactococcus* and *Streptococcus*. In addition, detection of potential pathogens differed among sampling sites, site 2 and 6, in spring, especially the proportion of *Lac. garvieae*, 33.5 % and 27.8 %, respectively.

Chinese mitten crab (*Eriocheir sinensis*)

Chinese mitten crab is an important species in South East Asia, and due to its high economic value it is widely farmed in China. Five studies assessing the GI tract of Chinese mitten crab identified the presence of LAB (Li et al., 2007; Chen et al., 2015; Zhang et al., 2016; Ding et al., 2017; Dong et al., 2018). Li et al. (2007) revealed uncultured *Lactococcus* sp. in the intestine of healthy and 1-year old wild Chinese mitten crab. Chen et al. (2015) explored the intestinal bacterial community of Chinese mitten crab farmed in Lake Tai, China, and displayed Latobacillales and Streptococcaceae by DGGE. Later, Zhang et al. (2016) evaluated the bacterial communities in water, gills and gut of wild caught *E. sinensis*, and showed that Tenericutes and Proteobacteria were the predominant gut phyla, but two OTUs showed high similarity to *Lactococcus*.

As white spot syndrome virus (WSSV) is an emerging problem in shellfish aquaculture industry, Ding et al. (2017) investigated the effect of WSSV infection on gut microbiota of Chinese mitten crab. Microbial DNA from 30 gut samples and revealed that the abundance of Latobacillales significantly decreased in WSSV infected Chinese mitten crab. In a study investigated the intestinal microbiota and expression of gut immunity genes, Dong et al. (2018) revealed that in fore-, mid- and hindgut, genus *Lactococcus* was one of the predominant genera, while the species was less abundant in mid- and hindgut, indicating that *Lactococcus* mostly colonize the foregut (FG). In addition to *Lactococcus* was *Lactobacillus* detected, the abundance was not specified.

Abalone (*Haliotis asinina*)

Sarkono et al. (2010) isolated four culturable presumptive LAB strains, identified as genus *Lactobacillus*, from the fluid of the digestive tract of abalone.

Giant lion`s paw scallop (*Nodipecten subnodosus*)

Nava-Hernández (2008) identified LAB strain NS61 from the gut microbiota of the giant lion's paw scallop by using cultivation, but no further information was presented. Later, Campa-Córdova et al. (2011), tested the strain as a probiotic for the oyster (*Crassostrea corteziensis*).

LAB isolated from hepatopancreas

In a study analyzing the effect of synbiotic (GOS and *Ent. faecalis* and *P. acidilactici*) feeding, Safari and Paolucci (2017) revealed low population levels of presumptive LAB in the hepatopancreas of control and GOS fed narrow-clawed crayfish.

LAB isolated from shellfish muscle

In their study evaluating six shellfish species, Japanese littleneck (*Venerupis philippinarum*), turbo (*Batillus cornutus*), Pacific oyster (*Crassostrea gigas*), Chinese venus (*Cyclina sinensis*), blue mussel (*Mytilus edulis*) and surf clam (*Mactra veneriformis*), Kang et al. (2016) revealed LAB from meat in all species, but no pathogens were detected. After testing for antibacterial activity towards several pathogens were four stains selected out of 65 presumptive *Lactobacillus* spp. isolated. 16S rRNA analysis revealed high similarity to *Lb. plantarum*. These LAB were further tested for bile salt- and acid tolerance and adhesion ability, and the authors suggested them as potential probiotics in shellfish aquaculture, but as no probiotic studies were carried out, further studies are needed.

In addition to the fact that several LAB strains have probiotic potential is has been revealed that certain species of LAB isolated from shellfish have the potential being causative agents of disease. In the early study of Cheng and Chen (1998), they isolated *Enterococcus seriolicida* from the muscle of diseased giant freshwater prawn, while Wang et al. (2008) isolated *Lac. lactis* subsp. *lactis* from diseased giant freshwater prawn muscle; a disease resulted in 100% mortality in two days.

Braïek et al. (2018) isolated *E. lactis* from raw white shrimp, and tested the isolate for antibacterial activities against several Gram-positive strains including *Enterococcus*, *Lactococcus*, *Micrococcus*, *Carnobacterium*, *Lactobacillus*, *Staphylococcus*, *Listeria* and *Bacillus*, five Gram-negative species and 12 fungi species, and revealed production of enterocins A, B and or P, proteolytic activity, tolerance to bile and good autoaggregation and coaggregation capacities.

PROBIOTIC LAB IN SHELLFISH

LAB as feed utilisation improvement

Dietary inclusion of probiotics in aquatic animals is known to enhance feed digestion and absorption because of their abilities to release several digestive enzymes (etc. proteases, amylases, and lipases) and nutrients (etc. vitamins, amino acids, and fatty acids). These substances may take part in digestive process and feed utilization, as well as on the assimilation of diet elements resulted in improvement of host's health and growth (e.g. Irianto and Austin, 2002a; Bolasina et al., 2006; Ray et al., 2012; Hoseinifar et al., 2018, 2019; Ringø et al., 2018). Several studies have revealed altered enzyme patterns due to the intake of LAB in shellfish (**Table 2**).

Protease and amylase secretion have been elevated in Pacific white shrimp after feeding the shrimp *Lactobacillus* sp. at different dietary levels; 5%, 10%, and 15% of basal diet (Wang et al., 2010). Dietary inclusion of *Lac. lactis* subsp. *lactis* isolated from shrimp's intestine significantly increased cellulose, lipase, amylase, and protease compared to the control (Adel

et al., 2017). The significant increase in these enzyme activities may improve digestion and nutrient absorption, which in turn contributes to increase growth performance (Wang et al., 2012). It is well-established that the stimulation of digestive enzyme activities in fish and shellfish fed LAB may be attributable to the improvement of gut maturation (Tovar et al., 2002), prevention of intestinal disorders, and pre-digestion of antinutrient factors displayed in the feedstuffs (Verschuere et al., 2000). Similarly, significant improvement of protease and amylase activities were observed in *L. vannamei* fed *P. pentosaceus* at dose of 10^7 and 10^8 CFU/g. The authors also mentioned that the increase in shrimp's growth parameter and feed utilisation may be due to increase in digestive enzyme activity induced by the probiotics. When discusing the mode of action, probiotics might have the highest effects on the shrimp's digestive system in the ealy stage of life cycl, such the larval and early post-larval stages (Kamarudin et al., 1994; Lovett and Felder, 1990; Vine et al., 2006), and particularly LAB as they could release a broad range of exoenzymes (Moriarty, 1998). Furthermore, the presence of probiotics in shrimp's intestinal tract may induce the production of endogenous enzymes or contribute to the total enzyme activity of the gut (Saeed Ziaei-Nejad et al., 2006). The higher level of enzyme activities as a result of probiotics consumption could enhance the digestion and obsorption of protein, starch, fat, and cellulose, which might increase growth of shrimp fed the probiotic supplemented diets *vs*. the control. Dietary inclusion of commercial probiotic, *Lb. plantarum* at 10^9 CFU mL^{-1} for 15 days significantly improved amylase, lipase, and pepsin activity of Pacific white shrimp. Recently, Du et al. (2019) revealed that dietary inclusion of *Lb. pentosus* significant increased trypsin, lipase, and α-amylase in *L. vannamei*, while Zuo et al. (2019) indicated that administration of *Lactobacillus* significantly improved protease, lipase, and amylase of Pacific white shrimp. The enzymes mention above are important shrimp digestive enzymes which play an important role in the assimilation of nutrition in shrimp's intestine (Muhlia-Almazán et al., 2003). The concentrations of digestive enzymes were usually used as indicator for evaluating the shrimp's food conversion efficiency and growth performance, and many studies have demonstrated that dietary inclusion of probiotics could increased activity of trypsin, lipase, and α-amylase enzymes (e.g. Ziaei-Nejad et al., 2006; Arena et al., 2007; Anand et al., 2014). Zuo et al. (2019) suggested enhanched enzyme actitities by supplementation of *Lactobacillus* might be due to enzyme secretions of *Lactobacillus* or by strengthened secretion from cells stimulated by the probiotic, or by the combinations of the two factors.

LAB as effective growth promoters in shellfish

The most importane goal of commercial aquaculture is to achieve fastest growth and low feeding input. To obtain the goal, the scientific community has developed different technologies that can boost growth performance of farmed animals by functional-additives and natural growth promoters (Katya et al., 2014; Hernández et al., 2016). In this respect, probiotics are of importance to obtain enhanched growth, improved health, and well-being aquatic animals, because they serve as nutrients source, vitamins and digestive enzymes, which in turn play an important role on feed utilization, nutrition absorption, and growth performance (Lauriano et al., 2016; Nath et al., 2018), and dietary inclusion of probiotic has been hypothesized to enhance the appetite or stimulate organisms' digestibility (Irianto and Austin, 2002b). Probiotics can enhance feed efficiency of fish and shellfish by stimulating the release of digestive enzymes and maintaining the balance or improving the intestinal bacterial commnity, which led to the improvement of nutrients absorption and utilization, as well as the survival and growth of the host (Irianto and Austin, 2002b; Ibrahem, 2015).

Several studies evaluating the effects of dietary inclusion of probiotics have revealed possible involvement of probiotics on the improvement of the intestinal microbiota balance as well as

involved in the production of extracellular enzymes which by turns enahnce the feed utilization and growth of the cultured species as they act as growth promoters (Giri et al., 2013; Ringø et al., 2018). Most studies using LAB in shellfish focus on growth performance and survival rate, for example; supplementation of *E. faecium* and *Lac. garvieae* at 10^7 CFU/mL significantly enhance specific growth rate of *P. monodon* (Swain et al., 2009). Similar results were revealed by Vieira et al. (2010) in a study with *L. vannamei* administrated by *Lb. plantarum* isolated from Pacific white shrimp intestine. Kongnum and Hongpattarakere (2012) indicated significant higher relative growth rate and survival rate, and lower FCR in *L. vannamei* fed 2–4 × 10^8 CFU g^{-1} feed *Lb. plantarum* for 6 weeks. Similarly, giant freshwater shrimp fed dietary inclusion of *Lb. plantarum* showed significant increase in weight gain, specific growth rate, feed conversion efficiency, protein efficiency ratio, and carcass protein content; whereas feed conversion ratio (FCR) significant decreased (Dash et al., 2014, 2015, 2016). 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 was observed in *M. rosenbergii* fed *Lactobacillus sporogenes* for 90 days (Seenivasan et al., 2014). Wang et al. (2010) revealed in a study using *Lactobacillus* sp. supplemented in *L. vannamei* diet; significant improved weight gain and specific growth rate, while FCR was reduced compared to the control treatment. Likely, significant increase larval survival rate was observed in Cortez oyster larvae (*Crassostrea corteziensis*) larvae fed dietary inclusion of LAB strain NS61 isolated from giant lion`s paw scallop at concentration of 10^4 and 10^5 CFU/mL (Campa-Córdova et al., 2011), but no significant different in larval final size was revealed. Recently, dietary administration *Lac. lactis* subsp. *lactis* and *P. pentosaceus* significantly enhanced growth performance and FCR of *L. vannamei* (Adel et al., 2017a, 2017b). Similarly, *Lb. pentosus* and *Lb. plantarum* inclusion in *L. vannamei* diets significantly improved growth performance and feed utilisation (Zheng and Wang, 2017; Zheng et al., 2017, 2018; Correa et al., 2018; Gao et al., 2018). It is known that LAB possesses high protein value, with a wide range of amino acids and trace elements. They are not only directly absorbed by the host as nutrients, but also secretes some SCFAs, vitamins, and other nutrients in order to maintain the host's gut ecological balance and enhance growth (e.g. Prieur et al., 1990; Verschuere et al., 2000; Irianto and Austin, 2002a). In addition, once the LAB adhere and colonized the intestine, they will release some digestive enzymes, such as cellulase, protease, and lipase into the host' intestinal tracts, and help the host digest residual food, which promotes the absorption of nutrients (Gallagher et al., 2001; Vine et al., 2006). Recently, Zuo et al. (2019) indicated that supplementation of *Lactobacillus* at 10^7 CFU g^{-1} for 27 days significant increased the body weight of *L. vannamei*. Combination of several probiotics have shown to improve growth performance in shellfish; for example, Wang et al. (2019) revealed that combination of *Lb. pentosus*, *Laccoccus fermentum*, *B. subtilis*, and *Saccharomyces cerevisiae* significantly improved growth performance and survival rate of *L. vannamei*, but no significant different in carcass composition was observed.

LAB improve disease resistance in shellfish

Probiotics have been proven as an effective tool for disease prevention in aquaculture (Hoseinifar et al., 2018; Ringø et al., 2018). Previously, antibiotics and chemotherapeutics were commonly applied for diseases prevention and treatment in aquaculture (Miranda et al., 2018), but the intensive applications of these substances have caused many adverse effects, such as the development of antibiotic-resistant bacteria, the residue of them in the aquaculture products, and the transferring of resistance genes from animals to human (Fair and Tor, 2014; Watts et al., 2017a; Santos and Ramos, 2018). As an alternative to antibiotics and chemotherapeutics,

functional feed-additives, such as probiotics, prebiotics, and medicinal plants have gained attention in aquaculture (e.g. Akhter et al., 2015; Reverter et al., 2017). Probiotics can interact with or antagonize other enteric bacteria by resisting colonization or by directly inhibiting and reducing adherance and colonisation of opportunistic pathogens (Chiu et al., 2017). They can also improve host's health and well-being via physiological or immune modulation (Butt and Volkoff, 2019). In addition, they can produce a wide range of efficient molecules, which possess bactericidal activity. These molecules can inhibit pathogenic bacteria in the host's intestinal tract and provide a barrier against the proliferation of opportunistic pathogens (e.g. Martínez Cruz et al., 2012; Seghouani et al., 2017; Hoseinifar et al., 2018; Ringø et al., 2018). The bioactive molecules produced during the bactericidal activity are antibiotics, bacteriocins, siderophores, enzymes (lysozymes, proteases), and/or hydrogen peroxide as well as organic acids (Verschuere et al., 2000; Hoseinifar et al., 2018; Ringø et al., 2018). The inhibition of intestinal related diseases has been demonstrated in several aquaculture species via dietary inclusion of probiotics in aquafeeds (Ringø et al., 2018; Wanka et al., 2018; Serra et al., 2019). Thus, it can be concluded that probiotics consumption can protect aquatic animals from infectious disease via the stimulation of immune systems. Dietary inclusion of *Lb. plantarum* significantly increased disease resistance of Pacific white shrimp and giant freshwater shrimp against *Vibrio alginolyticus, V. harveyi*, and *A. hydrophila, respectively* (Chiu et al., 2007; Vieira et al., 2010; Kongnum and Hongpattarakere, 2012; Dash et al., 2015; Pacheco-Vega et al., 2018). In case of *Lb. pentosus*, dietary inclusion significantly increased disease resistance of *L. vannamei* and *Haliotis discus hannai* against *V. vulnificus, V. rotiferianus, V. campbellii,* and *V. parahaemolyticus*, respectively (Zheng and Wang, 2017; Gao et al., 2018; Du et al., 2019). Similarly, administration of *Lb. acidophilus* and *Lactobacillus* significantly enhanced disease resistance of *L. vannamei* against *V. alginolyticus* and white spot syndrome virus, respectively (Sivakumar et al., 2012; Zuo et al., 2019). Resistance against *Vibrio penaeicida* and *V. anguillarum* was observed in *Marsupenaeus japonicus* and *L. vannamei* fed diet supplemented with *Lac. lactis* and *Lac. lactis* subsp. *lactis*, respectively (Maeda et al., 2014; Adel et al., 2017a). Supplementation of LAB strains from National Collection, Pune, India, was reported to improved disease resistance of *P. indicus* against *V. parahaemolyticus*; injected with 0.1 mL of 3 x 10^9 cells mL^{-1} (Ajitha et al., 2004). The probiotic bacterium, *P. acidilactici* supplemented in *Litopenaeus stylirostris* diets significantly enhanced disease resistance against *V. nigripulchritudo* (Castex et al., 2010). Combination of several probiotics in Pacific white shrimp diets, such as *E. faecium*, and *Lb. pentosus* or the combination of *Lb. pentosus, Lac. fermentum, B. subtilis*, and *S. cerevisiae* significantly improved disease resistance against *V. parahaemolyticus* (Sha et al., 2016; Wang et al., 2019), while the combination of *E. faecalis* and *E. faecium* showed significantly increased disease resistance of *L. vannamei* against *A. hydrophila* and *V. vulnificus* (Cui et al., 2017).

LAB effects on rearing water quality

The main obstacles in using antibiotics and chemotherapeutics to improve the rearing water quality in aquaculture is the emergence of antimicrobial-resistant bacteria (Akinbowale et al., 2006; Watts et al., 2017b), and as an alternative strategy; application of probiotics has been suggested. It has been reported that adding probiotics into water environment provided more favourable organisms than diet incorporation (Fuller, 1989). The interaction between water environment and aquacultured species have been considered as sustainable for aquaculture (e.g. Verschuere et al., 2000; Kesarcodi-Watson et al., 2008). The use of probiotics as a bioremediation tool to modulate the beneficial microorganism community and to inhibit pathogenic bacteria in the aquaculture environment led to the improvement aquatic animals'

health status and performance (Rao, 2007; Martínez Cruz et al., 2012). For this purpose, probiotics have been produced commercially in several reasonable and specific preparations for fish, shrimp, and molluscs farming operations (Wang et al., 2005), but few studies have been conducted using LAB in shellfish aquaculture. Adding *Lb. plantarum* directly into culture tank of *M. rosenbergii* revealed no effect on water quality (Dash et al., 2016). The synergistic elimilation of pathogens with simultaneous reduce ammonia, nitrite and nitrate concentration have been demonstrated in an *in vitro* assay using *Lb. plantarum* and *Lb. hilgardii* as potential probiotic (Ma et al., 2009). Nonetheless, water quality parameters were not improved compared to the control treatment. This finding may be due to that the experiment was conducted in small low density indoor system where the uneaten feed and faeces were removed and rearing water was exchanged frequently. Furthermore, the water quality was maintained in optimum range for *M. rosenbergii* culture. So, good management practice might masked the possible effect of *Lb. plantarum* on the water quality (Silva et al., 2012). Similarly, Correa et al. (2018) revealed that dietary inclusion of *Lb. plantarum* had no effects on water qualtiy and pathogens removal in *L. vannamei* culutre under biofloc system. In contrast, dietary inclusion of *Lb. plantarum* significantly improved water quality and reduced shrimp diseases, as well as environmental impact (Pacheco-Vega et al., 2018).

LAB against stressful conditions

Intensification aquaculture with high density, normally caused stress for fish and shellfish (Guardiola et al., 2018), as stress will weaken the immune system of the host, and increase their susceptibility to infectious diseases (Kennedy et al., 2016). Stress is determined as '*physical or chemical factors that cause bodily reactions that may contribute to disease or death*' (Rottmann et al., 1992). In addition to the physical and chemical stressors, the biological stress is defined as a '*nonspecific response of the body to any challenge*' (Selye, 1982). According to the above definitions, there are many different stressors that aquatic animals faced during cultivation, such as transportation, malnutrition, stocking density, rearing temperature, anoxia, hypoxia, hyperoxia, chemicals, pesticides, and water salinity (e.g. Akhtar et al., 2011, 2013; Lushchak, 2011; Dawood et al., 2015a, 2015b).

Besides pathogen pressure, farmed finfish and shellfish are normally subjected to environmental disruption that can seriously affect their physiological condition and increase the oxidative stress (Lesser, 2006; Balasch and Tort, 2019). Therefore, probiotics are incorporated in aquafeed diets to ameliorate the effect of these oxidative stress factors. Supplementation of *P. acidilactici* at 10^7 CFU g^{-1} feed for one month showed significantly improved antioxidant condition of *Litopenaeus stylirostris* (Castex et al., 2010). Hence, it is believed that probiotic consumption may promote the diet utilisation (Castex et al., 2008), and help to increase the absorption of dietary antioxidants from the feed. In addition, they play a vital role in antioxidant activity, as demonstrated for LAB (Kullisaar et al., 2002). Castex et al. (2010) assumed that anti-oxidative characteristics of a *Lactobacillus fermentum* strain may function as protective mechanisms in the intestinal microbial ecosystem and thus contribute to overcoming exo- and endogenous oxidative stressess. Recently, dietary inclusion of *Lb. plantarum* significantly increased the resistance against stress, when shrimp were exposed to acute low salinity (Zheng et al., 2017). Probiotics have been used as effective tool to enhance shrimp's ability against environmental stress (Yeh et al., 2010; Dong et al., 2013). It is known that there is a strickly order set of events occuring in order to help an organism response to the environemtal and physiological stressors. The most common mechanism is rapid changes in gene expression followed by the synthesis of proteins involved in adaptation (Zhou et al., 2010). Up-regulation of ProPO mRNA level was recorded in shrimp challenged by pathogens or environmental

stress. It can be inferred that ProPO plays a critical role in shrimp immunity (Gao et al., 2009). Likely, dietary inclusion of *Lb. pentosus* at different concentrations not only improves the antioxidant capacity of abalones, but also significantly decreases the MDA content. Furthermore, this inclusion can increase environmental adaptability, remain redox balance, and stimulate the immune function of abalone (Gao et al., 2018).

SHELLFISH IMMUNE SYSTEM

Various species of crustaceans, molluscs, and Echinodermata rely solely on innate immunity to fight against pathogens (Söderhäll et al., 1998; Zhang et al., 2004; McFall-Ngai et al., 2007; Loker et al., 2017). While further verification is required, some studies suggested that shellfish may also have an adaptive-like immune system (Arala-Chaves et al., 2000; Flajnik et al., 2004; Hibino et al., 2006; Kurtz et al., 2006; Vazquez et al., 2009; Chiaramonte et al., 2015; Song et al., 2015). Due to economic reasons, the immune systems of crustaceans, especially shrimp, are more heavily studied compared to molluscs or *Echinodermata*.

Shellfish contain phagocytic cells including dendritic cells, macrophages, and neutrophils. Dendritic cells and macrophages recognize microbe-derived molecules (microbe-associated molecular patterns, MAMPs) through pattern recognition receptors (PRRs) expressed on the cell surface or inside the cells. MAMPs include lipopolysaccharides, peptidoglycans, β-1, 3-glucans, lectins, and nucleic acids (Kaisho et al., 2004; Cerenius et al., 2010; Smith et al., 2010, 2018; Song et al., 2010; Sánchez-Salgado et al., 2017). Including Toll-like receptors (TRLs), 11 types of PRRs have been identified in shrimp (Wang et al., 2013). The presence of other types of PRRs, such as NOD-like receptors (NLRs) and RIG-like receptors (RLRs) need to be identified in shrimp and other shellfish species. The interaction between PRRs and MAMPs activates receptor-dependent signalling pathways, which results in innate immune responses: cytokine production and stimulation of phagocytosis, clotting proteins, apoptosis, antimicrobial proteins (AMPs), and the complement system (Kaisho et al., 2004; Cerenius et al., 2010; Smith et al., 2010, 2018; Song et al., 2010; Li et al., 2013; Sánchez-Salgado et al., 2017). C-type (Ca^{2+} dependent) lectins are most common in shellfish among the lectin groups. The carbohydrate recognition domain of lectins recognizes microbes determining the specificity (Rast et al., 2006; Vazquez et al., 2009; Sánchez-Salgado et al., 2017). Enzymatic defence systems, such as lysozymes, prophenoloxidase, and antioxidant enzymes are also crucial to combating numerous microbial infections. Activated defence enzymes cleave the peptidoglycan linkage between *N*-acetylmuramic acid and *N*-acetylglucosamine resulting in the elimination of microbes. Additionally, the enzymes inhibit melanin formation which is essential for microbe survival and reduce oxidative stress (Sritunyalucksana et al., 2000; Vazquez et al., 2009; Hauton, 2012; Chiaramonte et al., 2015). Phagocytic cells such as dendritic cells, monocytes, macrophages, and neutrophils engulf the microbes. Phagocytosis of microbes results in the direct killing inside phagocytes by lysosomal enzymes, reactive oxygen species, and nitric oxide (Battistella et al., 1996; Salzet et al., 2001; Cerenius et al., 2010; Hauton, 2012; Chiaramonte et al., 2015; Bouallegui, 2019). Clotting is a critical and rapid response required for sealing tissue injury, preventing pathogen infection via the damaged sites (Sritunyalucksana et al., 2000; Lee et al., 2002; Cerenius et al., 2011). Apoptosis is an essential cellular response to eliminate opportunistic harmful cells in shellfish, and apoptosis is highly regulated by numerous factors (Sokolova. 2009; Kiss, 2010; Menze et al., 2010). Antimicrobial peptides secreted from epithelial cells kill a broad range of Gram-positive and Gram-negative microbes (Vazquez et al., 2009; Hauton, 2012; Song et al., 2015; Smith et al., 2018). The complement system is also

an essential innate defense component. Although the presence of the complement system in shellfish has been reported, further investigation is required (Gross et al., 1999; Nonaka and Yoshizaki, 2004; Song et al., 2015; Smith et al., 2018; Bouallegui, 2019).

LAB EFFECTS ON CRUSTACEANS IMMUNE SYSTEM

Most of the studies of LAB effects have mainly focused on shrimp. The effects of LAB administration on the innate immune systems of crab, shrimp, and crayfish are summarized in **Table 3.**

Mud crab

The LAB, *Lb. plantarum* 7-40 originally isolated from fermented cabbage, kimchi, was fed to juvenile mud crab (0.97 g) as a powder-mixed diet (10^9 CFU/kg) for 28 days (Yeh et al., 2014), and the *Lb. plantarum*-fed crabs showed higher growth performance than control fed crab. When challenged with *V. parahaemolyticus* (10^5 CFU/crab), the crabs treated with *Lb. plantarum* revealed 17 % increase in survival compared to the control group. In addition, the *Lb. plantarum*-treated group showed slightly elevated levels of total hemocyte count, phagocytic activity, and phenoloxidase activity. In contrast, the levels of respiratory burst, superoxide dismutase, and glutathione peroxidase were not significantly different between the experimental and control group.

Blue swimming crab

Talpur et al. (2013) treated swimming crab larvae for 14 days with indigenous *Lb. plantarum* PPG-2-10-Talpur at three different concentrations: 1 x 10^6, 5 x 10^6, and 1 x 10^7 CFU/mL. The *Lb. plantarum*-treated group displayed increased survival, 9.5%, 10.8%, and 8.3%, respectively compared to the control group (~ 2.3%). Of note, there appears to be an ideal dose of *Lb. plantarum* for beneficial survival effects, as feeding a high concentration (1 x 10^7 CFU/mL) of *Lb. plantarum* PPG-2-10-Talpur caused a somewhat adverse effect on the larvae.

Pacific white shrimp

White shrimp were fed a diet containing *Lb. plantarum* 7-40 at two different concentrations: 10^7 CFU/kg and 10^{10} CFU/kg diet (Chiu et al., 2007). Immunological parameters were measured at different feeding periods: 24, 48, and 168 hours. After 24 hours of feeding, total hemocyte count, phenoloxidase activity, and respiratory burst were not significantly different between the *Lb. plantarum* diet groups and the control group. After feeding for 48 hours and 168 hours, the shrimp were challenged with *V. alginolyticus* (2~6 x 10^6 CFU/shrimp). The cumulative mortality of the shrimp was significantly reduced in the groups fed *Lb. plantarum* 7-40 (33.3% and 23.3%, respectively) compared to the control group (43.3%). At 48 hours of feeding, the *Lb. plantarum*-fed group showed significantly decreased total hemocyte count and phenoloxidase activity although these parameters enhanced after 168 hours of feeding. In contrast, the respiratory burst, clearance efficiency, and superoxide dismutase increased after 48 and 168 hours feeding. The gene expression levels of *prophenoloxidase* and *peroxinectin* were also significantly higher in the 168 hour-feeding groups.

Sha et al. (2016b) fed white shrimp for 2 or 3 weeks on diets containing a mixture of *Lb. pentosus* HC-2 and *E. faecium* NRW-2 (10^7 CFU/g); originally isolated from the gut of Chinese white shrimp. The probiotics-treated groups highly expressed *Penaeidins-3α (PEN-3α)* and *proPO* genes in the midgut. When challenged with *V. parahaemolyticus* ATCC17802, the probiotics-fed shrimp significantly increased survival rates (55.56%) compared to the control (31.11%).

Wang et al. (2019) isolated *Lb. pentosus* BD6 from pigeon faces, *Lb. fermentum* LW2 from Jingsi Lake water, and *S. cerevisiae* P13 from fermented peaches. The authors tested the immunological effects of these probiotics by feeding Pacific white shrimp with diets containing single or a mixture of the three bacteria in different concentrations (10^7, 10^8 and 10^9 CFU/kg) for 56 days. All test groups showed no significant differences in total hemocyte numbers, but the *Lb. pentosus* BD6 group and *S. cerevisiae* P13 group significantly increased phenoloxidase activity like the mixture-fed group. The respiratory burst activity was enhanced in all groups except the *Lb. fermentum* LW2 and the *S. cerevisiae* group. All test groups increased lysozyme activity except the *S. cerevisiae* P13 group. Superoxide dismutase activity and phagocytic activity were slightly increased in all test groups compared to the control group. When challenged with *V. alginolyticus* infection, cumulative mortalities were significantly decreased in all the probiotic-treated groups (*Lb. pentosus* BD6: 40.7%, *Lb. fermentum* LW2: 40%, and *S. cerevisiae* P13: 53.3%) in comparison to the control group (73.3%). Strain mixture did not seem to have an effect on the mortality rates, as the shrimp fed with the mixture showed a similar mortality rate to those of the single strain-fed groups.

A commercially available product, PrimaLac® which included *Lb. acidophilus*, *Lb. casei*, *E. faecium*, and *B. bifidium* was tested on white shrimp for 8 weeks at different doses: 0.25 g, 0.5, and 1.0 g/kg (Miandare et al., 2016). The genes of prophenoloxidase, lysozyme and antimicrobial peptides (*penaidian and crustin*) were expressed significantly higher in a dose-dependent manner.

Vieira et al. (2010) tested innate immune activities of autochthonous *Lb. plantarum* by feeding the bacteria (1.5×10^8 CFU/g) to Pacific white shrimp 4 times a day for 60 days. Although no difference was observed in the final body weight and natural death, total LAB numbers in the shrimp gut were highly increased after 20 days of feeding. When challenged with *V. harveyi*, the *Lb. plantarum*-supplemented group showed a significantly higher survival rate (65.7%) compared to that of the control group (39.9%).

Kuruma shrimp

Immunomodulatory role of autochthonous *Lb. lactis* D1813 was investigated by feeding Kuruma shrimp probiotic diets once a day for 14 days (Maeda et al., 2014). Both *Lb. lactis* D1813 groups (10^5 and 107 CFU/g) increased prophenoloxidase gene expression in the gut at 7 days of feeding. In contrast, the gene expressions of Anti-LPS factor, superoxide dismutase, and prophenoloxidase were marginally increased. When challenged by *V. penaeicida* (10^8 CFU/mL) at 14 days of feeding, the *Lb. lactis* D1813-fed group (10^5 CFU/g) exhibited an increased survival rate (61.75%) compared to the control group (28.3%).

Giant freshwater prawn

Immune modulatory effects of *Lb. plantarum* MTCC1407 were tested by feeding giant freshwater prawn at three different concentrations (10^7, 10^8, and 10^9 CFU/g) (Dash et al., 2014). After 90 days of feeding, the shrimp significantly improved the innate immune parameters in a dose-dependent manner: total hemocytes, phenoloxidase activity, respiratory burst, and hemolymph clearance efficiency. The *Lb. plantarum*-feeding groups showed significantly reduced cumulative mortalities (10^7 CFU/g: 60%, 10^8 CFU/g: 40%, and 10^9 CFU/g: 31.11%) compared to the control group (82.23%) when infected with *A. hydrophila* ATCC35654 (10^6 CFU/prawn). The same research group performed a similar study after heat-killing the same bacteria; at 60°C for 30 min (Dash et al., 2015). Giant freshwater prawns were fed heat-killed *Lb. plantarum* (10^7, 10^8, and 10^9 CFU/g) for 90 days. LAB administration significantly increased the innate immune parameters in a dose-dependent manner, and mortality rates decreased significantly (10^7 CFU/g group - 71%, 10^8 CFU/g - 46%, 10^9 CFU/g - 38%) compared to the control group (84%) when challenged with *A. hydrophila* ATCC35654 (10^6 CFU/prawn). Furthermore, the same research group tested the water additive effect of *Lb. plantarum* MTCC1407 by cultivating the shrimp in water supplemented the live bacteria for 90 days at three doses, 10^7, 10^8, and 10^9 CFU/L (Dash et al., 2016). When challenged with *A. hydrophila* ATCC35654 (10^6 CFU/prawn), the cumulative mortality rates of the LAB-treated group were reduced in a dose-dependent manner (10^7 CFU/L: 80%, 10^8 CFU/L: 73.33%, 10^9 CFU/L: 62.23%, and the control: 82.23%). In addition the immune parameters were enhanced in a dose-dependent manner as well.

Narrow-clawed crayfish

Innate immune activities of *P. acidilactici* and *E. faecalis* were investigated on narrow-clawed crayfish (Safari et al., 2017). Juvenile crayfish were fed diets containing *P. acidilactici* (3.4 x 10^7 CFU/g), *E. faecalis* (3.4 x 107 CFU/g), *P. acidilactici* + GOS (10g/kg), or *E. faecalis* + GOS (10g/kg) for 126 days. Crayfish fed the *E. faecalis* + GOS diet revealed highest activities of phenoloxidase, superoxide dismutase, lysozyme, and nitric oxide synthase. When infected by *A. hydrophila* ATCC49040 (1 x 10^8 CFU/mL), the mean survival rate of the crayfish fed with the *E. faecalis* + GOS diet was higher (77.67%) than that of the control group (8.33 %) and the other groups (58.33 ~ 72.33%).

LAB EFFECTS ON MOLLUSCA IMMUNE SYSTEM

The studies of LAB effects on mollusca are limited and are summarized in **Table 3**.

Kumamoto oyster (*Crassostrea sikamea*)

Abasolo-Pacheco et al. (2016) isolated *Lb. plantarum* C from winged pearl oyster and *L. graminis* RL5 from lion's paw scallop. The probiotic effects of these two LAB strains were tested by cultivating juvenile oysters in water containing LAB (1 x 10^6 CFU/mL) for 35 days. The oysters treated with the mixture of the isolates showed significantly higher growth rates compared to the control group, but it is hard to fully conclude as the growth rate was assessed with small size oysters (tens mg of body weights).

Catarina scallop (*Argopecten ventricosus*)

The LAB strains isolated from oyster (Abasolo-Pacheco et al., 2016) were tested for their probiotics effects on catarina scallop (Abasolo-Pacheco et al., 2017). Larvae and juveniles were treated every 48 hours with a single or combined strain of probiotics (1 x 10^6 CFU/mL) for nine days (larvae) and 21 days (juveniles). Early veliger larvae treated with *Lb. graminis* RL5 and antibiotics or *Lb. plantarum* C3 alone significantly improved survival and growth rates. The mixture of *Bacillus* (*B. cereus* PB1-1, *B. flexus* PB1-5, and *B. firmus* PB1-6 in 1:1:1 ratio) significantly enhanced survival of juveniles from *V. alginolyticus* CAIM57 challenge (1 x 10^7 CFU/mL) (60 %) compared to the control (0%), while juveniles treated with the LAB showed only 15% survival.

New Zealand abalone (*Haliotis iris*)

Autochthonous strains of probiotics (*Exiguobacterium* spp. JHEb1, *Vibrio* spp. JH1 and *Enterococcus* spp. JHLDc) were administered to farmed New Zealand abalone (Hadi et al., 2014). Juvenile abalones were fed for 60 days with diets containing the mix of two strains (2-p: *Exiguobacterium* spp. JHEb1 and *Vibrio* spp. JH1, 2 x 10^8 CFU/g) or the mixture of the three strains (3-P, 3 x 10^9 CFU/g). The probiotics-fed abalones significantly increased maximum shell length (3-P: 20.9%, 2-P: 15.4%) and wet weight (3-P: 19.8%, 2-P: 9.5%). In addition, both the 2-P and 3-P group displayed significantly lower mortalities (3.33%) than the control group (16.67%). Theses autochthonous strains were further investigated over a four-month period by feeding juvenile abalones (1% body weight per day) with the mixture of the three strains (2 x 10^9 CFU/g) (Grandiosa et al., 2018). The probiotics-fed group significantly improved in growth compared to that of the control: length (32.3% *vs*. 22.3%, width (31.9% *vs*. 20.9%) and wet weight (109.6% *vs*. 72.8%), respectively. Until 8 weeks of feeding, no significant differences in total hemocyte count and hemocyte viability were observed between the probiotics and the control group, but after 16 weeks of feeding, the probiotics-feeding group revealed significantly enhanced total hemocyte count and hemocyte viability. Furthermore, the probiotics group showed higher viability (90.8% *vs*. 75.6%) and a higher percentage of ROS-positive cells (19.4% *vs*. 0.5%) compared to the control.

LAB EFFECTS ON ECHINODERMATA IMMUNE SYSTEM

Echinodermata has a sophisticated immune system including coelomocytes, clot formation factors, Toll-like receptors, NOD-like receptors, other lectins, complement factors, and antimicrobial peptides (Smith et al., 2018), but studies evaluating LAB effects on the *Echinodermata* immune system are limited.

Sea cucumber (*Actinopyga echinites*)

Juvenile sea cucumbers were fed diets including three probiotic strains of similar ratio (*Lactobacillus*, *Sphingomonas*, and *Acetobacter*) at two different concentrations (6 x 10^7 and 9 x 10^7 CFU/g) for 90 days (Bao et al., 2017). The probiotics-fed sea cucumbers significantly enhanced growth performance in a dose-dependent manner (control group: 10.6 g, 6 x 10^7 CFU/g group: 14.9 g, 9 x 10^7 CFU/g group: 15.4 g). Immune parameters, such as superoxide dismutase, catalase, acid phosphatase, alkaline phosphatase, and lysozyme activity were also

enhanced in a dose-dependent manner, but administration of 6 x 10^7 CFU/g did not significantly altered in lysozyme activity compared to the control.

CONCLUSIONS

When investigating the GI tract microbiota, one major concern occurs; most studies evaluating the shellfish gut microbiota have focus to characterize the communities in the GI lumen (the allochthonous microbiota), while those bacteria that adhere to the mucosal surface (the autochthonous microbiota); which may be important in specialized physiological functions, remain less investigated. We therefore recommend more focus on the autochthonous gut microbiota of shellfish in future studies.

Compared to finfish studies where the gut microbiota have been investigated in different (FG, MG and hindgut) segments (Ringø et al., 2016; 2018), as differences may occur between the different segments. As limited numbers of studies have evaluated the bacterial community in the different intestinal segments of shellfish (Cheung et al., 2015; Ooi et al., 2017; Dong et al., 2018; Mongkol et al., 2018); scientists have to investigate the shellfish microbiota in different gut regions.

In shellfish GI tract the dominant LAB genera are *Lactobacillus*, *Lactococcus* and *Enterococcus*, while *Leuconostoc*, *Pediococcus*, *Streptococcus*, *Vagococcus*, *Weissella*, and *Carnobacterium* are generally seldom isolated.

In the comprehensive review of Ringø et al. (2016) the dietary effect of finfish on gut microbiota was investigated, but less information is available on this topic in shellfish, as only few studies have investigated the dietary effect; lipid and carbohydrate on the gut microbiota of shellfish (Zhang et al., 2014; Qiao et al., 2017; Sun et al., 2018, 2019). In addition, insight into the function of the shellfish intestinal microbiota are needed as few studies have focus on this topic (Cornejo-Granados et al., 2018; Gao et al., 2019a).

This review reveal that *Lactobacillus* sp., *Lactococcus* sp., *Pediococcus* sp., *Enterococcus faecalis*, *Bacillus subtilis*, *Saccharomyces* cerevisiae, and other LAB strains have a potential in contributing to the successful and sustainable of shellfish farming by remaining the health and well-being of cultured animals ranging from improvement of growth, feed utilization, protection against infectious diseases, as well as decreasing stresses and the environmental impact induced by aquaculture industry. In conclusion, further investigations are needed to elucidate the effects of LAB on gut microbiota, nutrition utilization, and molecular responses to help in understanding the exact mode of action of LAB in mentioned parameters.

It is essential to understand the shellfish immune system and its regulatory mechanism in order to identify the proper probiotic candidates and accurate assessments of immunomodulatory effects in specific shellfish. While there is relatively active research being done involving the shrimp immune system, the current status of shrimp immunology is still far immature in comparison to those of mammals. Most of the studies focused on the identification of pattern recognition receptors and the downstream signaling pathways. Information about innate immune regulatory mechanisms, cytokine-producing cells, and target cells of cytokines, regulatory mechanisms of cytokines, and their effects on innate immunity needs to be further explored. Another critical aspect to consider is in regards to the changes in gut microbiomes of shellfish due to probiotic feedings and its effect on the health of the host shellfish. It is likely that microbe-associated molecular patterns of the altered gut microbiome affect the shellfish immune system, which may influence the status of the health status of the host. In addition, SCFAs released from the gut microbiome, such as butyric acids, may also contribute to the immune regulation of shellfish.

AUTHORS CONTRIBUTIONS

ER: introduction, LAB in shellfish GI tract, editorial. HD: LAB as probiotics. SL and SS: immunology of LAB. All authors have approved the manuscript for publication.

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1696

1697 Table 1. Lactic acid bacteria (LAB) in the gastrointestinal (GI) tract, hepatopancreas and in muscle of shellfish, detected by culture based or culture-independent
1698 methods (C-IM).

Species	**Source**	**Isolated from**	**Methodology**	**Allo or auto**	**LAB identified**	**References**
Shrimp*	Natural/wild	GI tract	Cultivation	ni	*Lb. plantarum*[2]	Hongpattarakere et al., 2012
Giant freshwater prawn (*Macrobrachium rosenbergii*)	Natural/wild	GI tract	Cultivation	Allo+auto	*Lac. garvieae*, *P. acidilactici* and *E. faecium*	Cai et al., 1999[1]
	Natural/wild	GI tract	Cultivation	Allo+auto	*Enterococcus* spp.	Lalitha and Surendran, 2004
	Natural/wild	GI tract	Cultivation	Allo+auto	*Lactobacillus* spp.	Kennedy et al., 2006[1]
	Aquaculture	GI tract	Cultivation	Allo+auto	*Lactobacillus* sp.	Dash et al., 2014, 2016
Oriental river prawn (*Macrobrachium nipponense*)	Natural/wild	GI tract	C-IM	Allo+auto	*Lactobacillus* sp., *Leuconostoc* sp. and *Streptococcus* sp.	Tzeng et al., 2015
	Natural/wild	GI tract	C-IM	Allo+auto	Latobacillales* and Enterococcaceae*	Chen et al., 2017a
	Natural/wild	GI tract content	C-IM	Allo	*Lactobacillus* sp., Lactococcus sp., *Leuconostoc* sp., Carnobacteriaceae*, Aerococcaceae* and Enterococcaceae*	Zhao et al., 2018
Pacific white shrimp (*Litopenaeus vannamei*)	Aquaculture	GI tract	Cultivation	Allo+auto	LAB*	Viera et al., 2007[1]

	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* spp. and *Str. faecalis*	Zhou et al., 2007[1]
	Aquaculture	GI tract	Cultivation	ni	LAB*	Viera et al., 2008[1]
	Aquaculture	GI tract	Cultivation	Allo+auto	LAB*	Viera et al., 2010[1]
	Aquaculture	GI tract	Cultivation	Auto	*Lb. plantarum, Leu. mesenteroides* subsp. *mesenteroides/ dextranicum*	Kosin and Rakshit, 2010[1]
	Natural	GI tract content	Cultivation	Allo	LAB*	Kongnum and Hongpattarakere, 2012
	Aquaculture	GI tract	Cultivation	Allo+auto	LAB* and *Bifidobacterium* sp.	Boonanuntanasarn et al., 2016
	Aquaculture	GI tract	C-IM	Allo+auto	Lactobacillaceae* and Streptococcaceae*	Huang et al., 2016
	Aquaculture	GI tract	Cultivation	ni	*P. pentosaceus*[3] and *Lactobacillus* sp.	Adel et al., 2017a
	Aquaculture	GI tract	Cultivation	Allo+auto	*Lac. lactis* subsp. *lactis*[3] and *Lactobacillus* spp.	Adel et al., 2017b
	Aquaculture	GI tract	C-IM	Allo+auto	*Weissella* sp.	Chen et al., 2017b
	Aquaculture	GI tract content	C-IM	Allo	*Bifidobacterium* sp.	Cornejo-Granados et al., 2017
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp. and *Streptococcus* sp.	Duan et al., 2017
	Aquaculture	GI tract	C-IM	Allo	*Lactobacillus* sp.	He et al., 2017

	Aquaculture	Gut content	C-IM	Allo	*Carnobacterium* sp., *Lactococcus* sp., *Lactobacillus* sp., *Leuconostoc* sp., and *Streptococcus* sp.	Suo et al., 2017
	Aquaculture	GI tract	C-IM	Allo+auto	Lactobacillaceae*	Xiong et al., 2017
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp.	Zeng et al., 2017
	Aquaculture	GI tract	Cultivation	ni	LAB and *Lb. pentosus*[3]	Zheng and Wang, 2017
	Aquaculture	EI with content	Cultivation	Allo+auto	*Lb. plantarum* and *Lac. lactis*	Chomwong et al., 2018
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp. and *Lactococcus* sp.	Duan et al., 2018
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp. and *Streptococcus* sp.	Hou et al., 2018
	Aquaculture	GI tract	C-IM	Auto	*Lb. plantarum*	Huynh et al., 2019
	Aquaculture	Gut content	C-IM	Allo	Lactobacillaceae*	Pinoargote et al. 2018
	Aquaculture	GI tract	C-IM	Allo+auto	Lactobacillaceae*, Leuconostocaceae* and Streptococcaceae*	Xue et al., 2018
	Aquaculture	GI tract	C-IM	Allo	*Lactobacillus* sp.	Fan et al., 2019
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp. and *Streptococcus* sp.	Gao et al., 2019b
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactococcus* sp.	Pei et al., 2019
White shrimp (*Penaeus vannamei*)	Natural	GI tract	Cultivation	Allo	*Lb. plantarum*[3] and LAB*	Kongnum and Hongpattarakere, 2012

	Aquaculture	GI tract	C-IM	Allo+auto	*Lactobacillus* sp. and *Lactococcus* sp.	Sun et al., 2016
	Aquaculture	GI tract	C-IM	Allo+auto	*Lactococcus* sp., *Lac. garvieae* and Lactobacillaceae*	Gainza et al., 2018
Brown shrimp (Farfantepenaeus californiensis)	Aquaculture	GI tract	Cultivation	Allo+auto	*P. pentosaceus* and LAB*	Leyva-Madrigal et al., 2011
Indian white shrimp (*Penaeus indicus*)	ni	GI tract	Cultivation	Allo+auto	LAB*[4]	Gopalakannan, 2006
	Natural/ wild	GI tract	Cultivation	Allo+auto	*Str.* Phocae PI80[3]	Kanmani et al., 2010
Kuruma shrimp (*Marsupenaeus japonicus*)	Natural/ wild	GI tract	Cultivation	Allo+auto	*E. faecalis*, *E. faecium*, *E. pseudovium*, *E. raffinosus*, *Lactobacillus* sp. *Lb. plantarum*, *Lb. nagelii*, *Lac. garvieae*, *Lac. lactis*, *P. pentosaceus*, *Vc. campiphilus* and *Vc. fluvialis*	Maeda et al., 2014
Giant tiger prawn (*Penaeus monodon*)	ni	GI tract	Cultivation	Allo+auto	LAB*[4]	Gopalakannan, 2006
	ni	GI tract	Cultivation	Allo+auto	*Enterococcus* sp. S2[3]	Nimrat et al., 2013
	Natural/wild and aquaculture	GI tract	C-IM	Auto	*Lactobacillus* sp. and *Lactococcus* sp.	Rungrassamee et al., 2014

Yellow shrimp (*Metapenaeus brevicornis)*	Natural	GI tract	Cultivation	Allo	LAB*	Kongnum and Hongpattarakere, 2012
Chinese shrimp (*Fenneropenaeus chinensis*)	Aquaculture	GI tract	C-IM	Allo+auto	*E. faecalis*	Liu et al., 2011[1]
	Natural	MG	Cultivation	Allo+auto	LAB*	Sha et al., 2016 b
Banana shrimp (*Fenneropenaeus* merguiensis)	Natural	GI tract	Cultivation	Allo	LAB*	Kongnum and Hongpattarakere, 2012
European lobster (*Homarus gammarus*)	Aquaculture	GI tract	Cultivation and C-IM	Allo+auto	*W. confusa* and *W. cibaria*	Daniels et al., 2010[1]
	Aquaculture	GI tract	C-IM	Allo+auto	*W. confusa* and *W. cibaria*	Daniels et al., 2013[1]
Narrow clawed crayfish (*Astacus leptodactylus*)	Aquaculture	GI tract	Cultivation	Auto	LAB*	Nedaei et al., 2019
Mud crab (*Scylla paramamosain*)	Aquaculture	GI tract	C-IM	Allo+auto	*Str. mutans* (diseased), *W. fabaria* (farmed) and bacterium Latobacillales 1247 (hatchery)	Li et al., 2012[1]
Swimming crab (*Callinectes* sp.)	Natural/wild	GI tract	Cultivation	Allo+auto	*S. agalactiae*	Uaboi-Egbenni et al., 2010[1]
Blue swimming crab (*Portunus pelagicus*)	Natural/wild	GI tract	Cultivation	Allo+auto	*Lb. plantarum*[3], *Lb. salivarius*[3], *Lb. rhamnosus*[3], *W. confusa* and *W. cibaria*	Talpur et al., 2012[1]

Swimming crab (*Portunus trituberculatus*)	Natural/wild	GI tract	C-IM	Allo+auto	*Carnobacterium, Lactococcus, Streptococcus* and *Vagococcus*	Kim et al., 2017
Chinese mitten crab (*Eriocheir sinensis*)	Aquaculture	GI tract	C-IM	Allo+auto	Uncultured *Lactococcus* sp.	Li et al., 2007
	Aquaculture	GI tract	C-IM	Auto	Latobacillales*	Chen et al., 2015
	Natural/wild	GI tract content	C-IM	Allo	*Lactococcus* sp.	Zhang et al. 2016
	Natural/wild	GI tract	C-IM	Allo+auto	Latobacillales*	Ding et al., 2017
	Natural/wild	GI tract (FG, MG and HG)	CI-M	Allo+auto	*Lactobacillus* sp. and *Lactococcus* sp.	Dong et al., 2018
Abalone (*Haliotis asinina*)	Aquaculture	GI tract	Cultivation	Allo		Sarkono et al., 2010[1]
Giant lion`s paw scallop (*Nodipecten subnodosus*)	Aquaculture	GI tract	Cultivation	Allo+auto	LAB strain NS61[3]	Nava-Hernández, 2008[1]
	Aquaculture	GI tract	Cultivation	Allo+auto	*Lb. graminis*[4] and *Lb. plantarum*[4]	Abasolo-Pacheco et al., 2016
Narrow clawed crayfish	Aquaculture	Hepatopancreas	Cultivation	Auto	Presumptive LAB	Safari and Paolucci, 2017
Giant freshwater prawn	Aquaculture	Muscle	Cultivation	_____	*E. seriolicida*	Cheng and Chen, 1998[1]
	Aquaculture	Muscle	Cultivation	_____	*Lac. lactis* subsp. *lactis*	Wang et al., 2008[1]

Shortnek clam *(Tapes philippinarum*)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4] and *Lb. plantarum*[4]	Kang et al., 2016
Turbo (Batillus cornutus)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4]	Kang et al., 2016
Chinese venus (*Cyclina sinensis*)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4]	Kang et al., 2016
Blue mussel (*Mytilus edulis*)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4]	Kang et al., 2016
Surf clam (*Mactra veneriformis*)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4]	Kang et al., 2016
Pacific oyster (*Crassostrea gigas*)	Natural/wild	Muscle	Cultivation	_____	*Lactobacillus* sp.[4] and *Lb. plantarum*[4]	Kang et al., 2016
White shrimp	Aquaculture	Raw shrimp	Cultivation	_____	*E. lactis*[4]	Braïek et al., 2018

1699 Genera abbreviations: *E*. – *Enterococcus*; *Lac.* – *Lactococcus*; *Lb*. – *Lactobacillus*; *P*. – *Pediococcus*; *Str*. – *Streptococcus*; Vc. – *Vagococcus*; W. – *Weissella*

1700 [1] studies discussed in the review of Merrifield et al. (2014); [2] exopolysaccharides produced; [3] used as probiotics; [4] potential probiotics; *no further information
1701 was given; ni – no information available.

1702 FG - foregut; MG – midgut; HG - hindgut

1703

1704 Table 2. LAB used as probiotics in shellfish.

Species	Isolated from	Doses and duration	Shellfish species	Parameters investigated	References
LAB strains	National Collection, Pune, India	5×10^6 cells·g^{-1}, 4 weeks	*Penaeus indicus*	Resistance against *V. parahaemolyticus* ↑	Ajitha et al., 2004[1]
LAB strain NS61	Giant lion`s paw scallop, *Nodipecten subnodosus*	1×10^4 and 1×10^5 CFU/mL	*Cortez oyster larvae, Crassostrea corteziensis*	Larval survival rate ↑ Larval final size →	Campa-Córdova et al., 2011
Lactobacillus sp.	Intestine of *L. vannamei*	10^7 CFU g^{-1} 27 days	*Litopenaeus vannamei*	Digestive enzyme ↑ Body weight ↑ Resistance against WSSV ↑	Zuo et al., 2019
Lb. acidophilus	Homemade curd isolate	10^5 CFU g^{-1}	*Penaeus monodon*	*Resistance against V. alginolyticus* ↑	Sivakumar et al., 2012[1]
Lb. bulgaricus	Intestine of *L. vannamei*	10^7 and 10^9 cfu g^{-1}, 30 days	*L. vannamei*	Immune response and disease resistance ↑	Roomiani et al., 2018
Lac. lactis	Intestine, *Marsupenaeus japonicus*	10^5 cfu g^{-1}	*Marsupenaeus japonicus*	Resistance to *Vibrio penaeicida* ↑	Maeda et al., 2014
Lac. lactis subsp. *lactis*	Intestine, *L. vannamei*	10^6, 10^7, and 10^8 CFU g^{-1}	*L. vannamei*	Growth performance ↑ Activities of digestive enzymes ↑ *Lactobacillus* and *Bacillus* counts ↑ *Vibrio* counts ↓ *Resistance against V. anguillarum* ↑	Milad Adel et al., 2017
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 ↑ Resistance against *V. parahaemolyticus* ↑	Gao et al., 2018

Lb. pentosus	Gut of *Chaeturichthys stigmatias*	5×10^8 CFU g feed^{-1} 4 weeks	*L. vannamei*	Digestion related enzymes Resistance against *V. parahaemolyticus* ↑ Induced stress response genes expression ↑	Du et al., 2019
Lb. plantarum	Intestine of *L. vannamei*	10^8 CFU mL^{-1} 60 days	*L. vannamei*	Shrimp survival → *Vibrio* spp. count → Total lactic bacteria ↑ Resistance against *V. harveyi* ↑	Vieira et al., 2010[1]
Lb. plantarum	Intestine of *L. vannamei*	2-4 × 10^8 CFU g^{-1} feed 6 weeks	*L. vannamei*	Relative growth rate ↑, FCR ↓ Survival rate ↑ Hemocytes count ↑ Resistance against *V. harveyi* ↑	Kongnum and Hongpattarakere, 2012
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 ↑	Dash et al., 2014
Lb. plantarum	Culture collection	10^7, 10^8, and 10^9 CFU g^{-1} diet 90 days	*M. rosenbergii*	WG, SGR, FCE, PER ↑ FCR ↓, Carcass protein content ↑ Resistance against *Aeromonas hydrophila*	Dash et al., 2015
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
Lb. plantarum	Shrimp intestine	1.0 x 10^7 CFU mL^{-1} 35 days	*L. vannamei*	Growth performance → Water quality →	Correa et al., 2018
Lb. plantarum		20 × 10^3 cells mL^{-1}and 1 × 10^8 (CFU) mL^{-1}	*L. vannamei*	Improve water quality in biofloc system ↑ Reduce shrimp diseases and environmental impact ↓	Pacheco-Vega et al., 2018
Lb. plantarum	Commercial probiotic	10^9 CFU mL^{-1} 15 days	*L. vannamei*	Final weight, WG, SGR ↑, FCR ↓ Digestive enzyme activities ↑ Enterocytes height ↑	Zheng et al., 2018
Lb. plantarum	Commercial probiotic	10^9 CFU mL^{-1} 45 days	*L. vannamei*	Final weight, WG, SGR ↑, FCR ↓ Improved the resistance against the stress of acute low salinity ↑	Zheng et al., 2017

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)
P. acidilactici	Commercial probiotic	10^7 CFU g^{-1} of feed 1 month	*Litopenaeus stylirostris*	Antioxidant status ↑ Resistance against *V. nigripulchritudo* ↑	Castex et al., 2010[1]
P. pentosaceus	Intestine of *L. vannamei*	0, 10^6, 10^7, and 10^8 CFU/g diet 8 weeks	*L. vannamei*	Final weight, final length, WG, SR, WG ↑ FCR ↓ Protease and amylase activities ↑ *Lactobacillus* sp. and *Bacillus* sp. intestinal count ↑	Adel et al., 2017
E. faecium and *Lb. pentosus*	Gut of *Fenneropenaeus chinensis*) and *Chaeturichthys stigmatias*	1 × 10^7 CFU g $feed^{-1}$	*L. vannamei*	*Resistance against V. parahaemolyticus* ↑	Sha et al., 2016b
E. faecalis and *E. faecium*	Intestine of Prawn and mullet	-	*L. vannamei*	Resistance against *A. hydrophila* and *V. vulnificus* ↑	Cui et al., 2017
Lb. pentosus, *Lac. fermentum*, *Bacillus subtilis*, *Saccharomyces cerevisiae*	Commercial probiotic	10^7, 10^8 and 10^9 CFU $(kg\ diet)^{-1}$ 56 days	*L. vannamei*	Growth performance ↑ Survival rate ↑, Carcass composition → Resistance against *V. parahaemolyticus* ↑	Wang et al., 2019

Genera abbreviations: *E.* – *Enterococcus*; *Lac.* – *Lactococcus*; *Lb.* – *Lactobacillus*; *P.* – *Pediococcus*; *Str.* – *Streptococcus*; W. – *Weissella*; *V.* – *Vibrio*.

Weight gain (WG), Specific growth rate (SGR), Food conversion efficiency (FCE), Food conversion ratio (FCR), Protein efficiency ratio (PER), Survival rate (SR)

[1] studies discussed in the review of Hoseinifar et al. (2018)

1709 Table 3. Changes in Immunological parameters of shellfish by LAB treatment.

Shellfish phylum	LAB species	Experimental animals (weight)	Administration routs and dose	Administration length	Immune parameter changes	References
Crustacean	*Lb. plantarum* 7-40	Juvenile mud crab (*Scylla paramamosain*) (0.97 ± 0.14 g)	Diet, 10^9 CFU/kg feeding	28 days	Survival rate against *Vibrio parahaemolyticus* (10^5 CFU/crab) ↑, Total hemocyte count ↑, Phenoloxidase activity ↑, Phagocytic activity ↑	Yeh et al., 2014
		Intermolt stage white shrimp (stage C) (*Litopenaeus vannamei*) (Weight is not mentioned)	Diet, 10^7, 10^{10} CFU/kg feeding	14 days	Until 48 h: Total hemocyte count ↓, Phenoloxidase activity ↓, After 48 h: Respiratory burst ↑, Superoxide dismutase activity ↑, Clearance efficiency ↑, Prophenoloxidase mRNA ↑, Peroxinectin mRNA ↑	Chiu et al., 2007
	Lb. plantarum PPG-2-10-Talpur	Swimming crab larvae zoea 1 (Z-1) (*Portunus pelagicus*)	Immersion 1, 5, 10 x 10^6 CFU/mL	14 days	Survival rate ↑	Talpur et al., 2013

		(Weight is not mentioned)				
	Lb. pentosus HC-2	White shrimp (*Litopenaeus vannamei*) (3.5 ± 0.06 g)	Diet, 10^7 CFU/g feeding	2 weeks and 4 weeks	Midgut: Penaeidins-3α mRNA ↑, Prophenoloxidase mRNA ↑, Hepatopancreas: Prophenoloxidase mRNA ↑, Crustin mRNA ↑, Lysozyme mRNA ↑	Sha et al., 2016b
	E. faecium NRW-2				Midgut, Penaeidins-3α mRNA ↑, Prophenoloxidase mRNA ↑, Lysozyme mRNA ↑, Crustin mRNA ↑, Hepatopancreas: Crustin mRNA ↑, Lysozyme mRNA ↑	
	Lb. pentosus BD6	Juvenile white shrimp (*Litopenaeus vannamei*) (0.21 ± 0.01 g)	Diet, 4.1 x 10^9 CFU/kg feeding	56 days	Survival rate against *Vibrio alginolyticus* (10^5 CFU/shrimp) ↑, Phenoloxidase activity ↑, Respiratory burst ↑,	Wang et al., 2019

					Lysozyme activity ↑, Phagocytic activity ↑	
	Lb. fermentum LW2		Diet, 0.9 x 10^9 CFU/kg feeding		Survival rate against *V. alginolyticus* (10^5 CFU/shrimp) ↑, Lysozyme activity ↑, Superoxide dismutase activity ↑, Phagocytic activity ↑	
	S. cerevisiae P13		Diet, 1.6 x 10^9 CFU/kg feeding		Survival rate against *V. alginolyticus* (10^5 CFU/shrimp) ↑, Phenoloxidase activity ↑, Phagocytic activity ↑	
	Multi-LABs (*Lb. acidophilus*, *Lb. casei*, *E. faecium* and *B. bifidium*) (strains are not mentioned)	Juvenile white shrimp (*Litopenaeus vannamei*) (0.47 ± 0.02 g)	Diet, 0.25, 0.5, 1.0 g/kg feeding	60 days	Prophenoloxidase mRNA ↑, Lysozyme mRNA ↑, Penaidian mRNA ↑, Crustin mRNA ↑	Miandare et al., 2016
	Lb. plantarum	Post-larvae white shrimp	Diet, 1.5 x 10^8 CFU/g feeding.	60 days	Survival rate against *Vibrio harveyi* (2.5 x 10^5 CFU/shrimp) ↑, Total hemocyte count ↑,	Vieira et al., 2010

		(*Litopenaeus vannamei*) (0.08 ± 0.01 g)			Phenoloxidase activity ↑, Agglutinating activity ↑	
	Lac. lactis D1813	Kuruma shrimp (*Marsupenaeus japonicus*) (4.7 ± 0.3 g)	Diet, 10^5, 10^7 CFU/g feeding	7 days	Survival rate against *Vibrio penaeicida* (10^8 CFU/mL) ↑, Intestine: Crustin mRNA ↑, Anti-LPS factor mRNA ↑, Lysozyme mRNA ↑, Superoxide dismutase mRNA ↑, Prophenoloxidase mRNA ↑, Toll-like receptor 1 mRNA ↑ Hepatopancreas: Anti-LPS factor mRNA ↑, Lysozyme mRNA ↑	Maeda et al., 2014
	Lb. plantarum MTCC1407	Juvenile giant freshwater prawn (*Macrobrachium rosenbergii*)	Diet, 10^7, 10^8, 10^9 CFU/g feeding	90 days	Survival rate against *Aeromonas hydrophila* (10^6 CFU/prawn) ↑, Total hemocyte count ↑, Phenoloxidase activity ↑,	Dash et al., 2014
			Immersion, 10^7, 10^8, 10^9 CFU/L			Dash et al., 2016

	Heat-killed *Lb. plantarum* MTCC1407	(0.54 ± 0.03 g)	Diet, 10^7, 10^8, 10^9 CFU/g feeding		Respiratory burst ↑, Hemolymph clearance efficiency ↑	Dash et al., 2015
	P. acidilactici (strains are not mentioned)	Juvenile narrow-clawed crayfish (*Astacus leptodactylus*) (6.17 ± 0.03 g)	Diet, 7.53 log CFU/g feeding	126 days	Survival rate against *A. hydrophila* (10^8 CFU/mL) ↑, Total hemocyte count ↑, Phenoloxidase activity ↑, Superoxide dismutase activity ↑, Lysozyme activity ↑, Nitric oxide synthase activity ↑	Safari et al., 2017
	E. faecalis (strains are not mentioned)		7.53 log CFU/g feeding			
Mollusca	*Lb. graminis* RL5 / *Lb. plantarum* C	Juvenile Kumamoto oyster (*Crassostrea sikamea*) (37.33 ± 0.07 mg)	Immersion, 10^6 CFU/mL	35 days	*Vibrio* spp. Inhibitory activity ↑	Abasolo-Pacheco et al., 2016
	Lb. graminis RL5 / *Lb. plantarum* C	Catarina scallop (*Argopecten ventricosus*) (13.3 ± 0.03 mg)	Immersion, 10^6 CFU/mL	21 days	Survival rate against *V. alginolyticus* (10^7 CFU/mL) ↑, Superoxide dismutase activity ↓	Abasolo-Pacheco et al., 2017
	Enterococcus spp. JHLDc	New Zealand abalone (*Haliotis iris*)	Diet, 3 x 10^9 CFU/g feeding	60 days	Survival rate ↑	Hadi et al., 2014

	(mixed with *Exiguobacterium* spp., *Vibrio* spp.) (species are not mentioned)	(Weight is not mentioned)				
		New Zealand abalone (*Haliotis iris*) (2.14 ± 1.19 g)	Diet, 2 x 10^9 CFU/g feeding	16 weeks	Total hemocyte count ↑, Hemocyte viability ↑, Reactive oxygen species resistant-hemocyte count ↑, Non-apoptotic cell ↑, Early, late apoptotic cell ↓	Grandiosa et al., 2018
Echinodermata	*Lactobacillus,* (mixed with *Sphingomonas* and *Acetobacter*) (species are not mentioned)	Sea cucumber (*Apostichopus japonicus*) (0.63 ± 0.13 g)	Diet, 6, 9 x 10^7 CFU/g feeding	90 days	Superoxide dismutase activity ↑, Catalase activity ↑, Acid phosphatase activity ↑, Alkaline phosphatase activity ↑, Lysozyme activity ↑	Bao et al., 2017

General abbreviations: *E*. – *Enterococcus*; *Lac*. – *Lactococcus*; *Lb*. – *Lactobacillus*; *P*. – *Pediococcus*; *Str*. – *Streptococcus*, *W*. – *Weissella*; *B*. – *Bifidobacterium*.