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Host-associated probiotics, a key factor in sustainable aquaculture?

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Abstract

The aquaculture industry has dramatically developed during the last two decades. However, this development has, in some cases, resulted in environmental degradation, emergence of diseases and low productivity. The need for improving disease resistance, growth performance, feed efficiency, and safe aquatic production for human consumption has stimulated development and applications of probiotics in aquaculture. Probiotics used in aquaculture include genera of *Bacillus*, *Lactobacillus*, *Enterococcus*, and *Carnobacterium*, and yeast. However, most of these probiotics are derived from terrestrial sources and not from the environment in which the aquatic animals live or the host animal. The use of "host-associated probiotics" has recently gained attention, as they offer an alternative strategy within aquaculture, which *per se* is dependent on the use of terrestrial microorganisms. The benefits of host-associated probiotics include improved growth performance, feed value, enzymatic contribution to digestion, inhibit adherence and colonization of pathogenic microorganisms in the gastrointestinal tract, increase hematological parameters, and immune response.

The present review addressed insight into the application of host-associated probiotics within aquaculture, with special focus on their immunomodulatory and growth enhancing effects. Furthermore, the current review discusses research gaps and issues that merit further investigations.

Keywords: Host-associated probiotics, Sustainable aquaculture, Immunomodulation, Growth promoter, Terrestrial microorganisms; Disease resistance

1. Introduction

Aquaculture is the fastest growing animal protein sectors to meet the demands of today's growing worldwide population. For the satisfaction of the increased human consumption, intensive aquaculture systems at high densities have been developed (Tal et al., 2009). This intensification has however, resulted in significant damage to the aquaculture environment, due to organic wastes production which consume dissolved oxygen in ponds, and increase toxic metabolites; responsible for high mortality (Martinez Cruz et al., 2012). For long time, chemotherapies and antibiotics were applied as an effective remedy for disease outbreaks in aquatic animals (Serrano, 2005). However, due to their excessive use, aquatic pathogens have become resistant to such treatments, along with the suppression of the host's immune system (Capkin et al., 2015, 2017; Dawood & Koshio, 2016). Furthermore, the application of antibiotics may extend to human consumption, which could adversely affect human health and weaken the immune systems (Cheng et al., 2014; Hoseinifar et al., 2015; Langdon et al., 2016). As a result, strict regulations against antibiotic administration in livestock-, poultry-, and the aquaculture sector have been established in several countries. Alternative strategies such as; vaccines, pro -, pre -, synbiotics, and medicinal herbs must further be investigated to improve health of aquatic animals (Martínez Cruz et al., 2012; Altinok et al., 2015; Adel et al., 2016; Abdelkhalek et al., 2017; Van Doan et al., 2017; Dawood et al., 2018).

Host aquatic microorganisms play a crucial role in the health maintenance by boosting the immune system, and increasing the resistance against opportunistic pathogens via the production of antimicrobial substances (e.g. Llewellyn et al., 2014; Ibrahem, 2015; Yan et al., 2017). When discussing the functionality of gut microbiota, it depends on the ability of microorganisms to interact within the gastrointestinal (GI) tract, which benefit the host through influence upon its biological functions (Ramírez & Romero, 2017).

For nearly half a century the word probiotic has been used in several different ways, since Lilly & Stillwell (1965) first used it. Gatesoupe (1999) defined probiotics as "*live microbial feed supplements that improve the health of both humans and terrestrial livestock*", and according to Dawood et al. (2016), probiotics is required to maintain a healthy environment for aquatic animals and to increase their performance, without any negative impacts upon the consumers. Supplementation of aquatic animal diets with probiotics positively influences growth performance, feed utilization, physiological conditions, optimize cell proliferation under stressful conditions, promote immune cell stimulation, modulate the gut microbiota and improve disease resistance (e.g. Irianto & Austin, 2003; Merrifield et al., 2010; De et al., 2014; Ringø et al., 2014; Hai, 2015a).

When discussing disease resistance, the importance of a stable microbiota is worth to mention. The best evidence for this protective effect of the gut microbiota stems from an early study revealing that germfree animals are more susceptible to diseases compared to corresponding conventional animals with a "complete gut microbiota" (Collins & Carter, 1978). Germfree mouse can be killed with 10 cells of *Salmonella enteritidis* whereas 10^6 cells are needed to kill conventional mouse with a conventional gut microbiota. Therefore, it is crucial to increase our knowledge on probiotics adhering and colonising the GI tract of endothermic animals as well as aquatic animals, in the context of improved growth performance and health.

When discussing the importance of probiotics in aquaculture, the mode of action and their effects on the intestinal microbiota, immunological, physiological responses, as well as growth performance must be continually investigated. Recently, there has been increasing attention towards administration of host-associated probiotics in aquaculture (Lazado et al., 2015; Li et al., 2018). However, as no clear definition *per se* exist, we defined host-associated probiotics as; bacteria originally isolated from the rearing water or the GI tract of the host to improve growth and health of the host. In aquaculture, *per se* it is not clear, whether host-associated probiotics are more effective than probiotics from other origins, even though there is some evidence demonstrating beneficial effects of host-associated probiotics *vs*. probiotics isolated from other sources (Lazado et al., 2015). One possible reason for their superior function may be because they perform better within their own original environment. Therefore, the present review addressed on the health benefits of host-associated probiotics in aquaculture, and their potential immunomodulatory and growth promoting effects.

2. Sustainable aquaculture: the role of probiotics

Outbreaks of infectious diseases are a major obstacle for the development of aquaculture, which adversely affect the sustainability of this industry (Mardones et al., 2018). Throughout the last decades, the aquaculture industry was heavily dependent on the use of antibiotics and chemotherapeutics for diseases control and prevention (Romero et al., 2012; Fečkaninová et al., 2017). However, the abusive use of these substances caused many adverse effects upon the host and its environment (e.g. Romero et al., 2012; Miller et al., 2016; Capkin et al., 2017; Suzuki et al., 2017), and therefore development of alternative strategies to antibiotics and chemotherapeutics are needed (e.g. Defoirdt et al., 2011; Altinok et al., 2016; Founou et al., 2016).

Sustainable aquaculture has been created to preserve and develop the industry (Bostock et al., 2010). In this context, several criteria have been put forward and include; vaccines, immunostimulants, pro -, pre - and synbiotics (e.g. Ringø et al., 2014; Lazado et al., 2015; Hoseinifar et al., 2016). Several types of vaccines have been developed for aquaculture, in which the most successful effects are reported in salmonids and cyprinids (e.g. Dhar et al., 2014; Ringø et al., 2014; Lazado et al., 2015; Hoare et al., 2017). Recent findings have revealed that vaccines are effective for disease control in aquaculture (e.g. Johnson et al., 2008; Brudeseth et al., 2013; Assefa & Abunna, 2018). However, individual vaccines are known to be effective against only one type of pathogen; which limiting their use in aquaculture (Ardó et al., 2008; Feodorova et al., 2014). Immunostimulants with a wide range of applications and functions have therefore, been considered as an alternative strategy to overcome the “drawback” of vaccines (Barman et al., 2013; Hoseinifar et al., 2017). These bioactive compounds boost the immune system of the host, and protect the host against wide range of pathogens (e.g. Bricknell & Dalmo 2005; Ringø et al., 2012; Hoseinifar et al., 2015; Nawaz et al., 2018).

Probiotics have many beneficial properties to the host and its environment, and they are now widely used in aquaculture as growth promoters, immunostimulants, and for disease protection (Pérez-Sánchez et al., 2014; Hai, 2015b). The word *probiotic* stems from the Greek roots *pro* and *bios*, or “*profile”* (Schrezenmeir & de Vrese, 2001). As a concept, the use of probiotics to control disease is referred to as “the use microorganisms against microorganisms” (Lazado et al., 2015). During the last two decades, numerous comprehensive reviews have addressed on probiotics and their impacts in aquaculture (e.g. Gatesoupe 1999; Verschuere et al., 2000; Irianto & Austin, 2003; Balcázar et al., 2006; Merrifield et al., 2010; Pérez-Sánchez et al., 2014; Ringø et al., 2014; Hai, 2015a,b; Hoseinifar et al., 2016) with multidimensional actions. Probiotics offer numerous beneficial effects, including immunomodulatory, nutritional, and environmental capacity, and therefore have a great competitive advantage as prophylactic against disease (Ohashi & Ushida, 2009; Lazado et al., 2015). While there is no concrete evidence to conclude that probiotics are better than immunostimulants or vaccines, the beneficial effects upon the host and their environment ensure that probiotics will remain one of the most promising approaches used to control diseases and the subsequent environmental modifiers (Newaj-Fyzul & Austin, 2015). Several probiotics species are used in aquaculture; e.g. *Bacillus* sp., *Lactobacillus* sp., *Enterococcus* sp., *Streptomyces, Carnobacterium* sp., and yeast (e.g. Gatesoupe, 2007; Martínez Cruz et al., 2012; Tan et al., 2016; Elshaghabee et al., 2017). Table 1, 2 and 3 summarize the results of studies from 2005 to 2018, focusing on the effects of host-associated probiotics as growth promoters and immunostimulants in aquaculture.

3. Host-associated *vs*. terrestrial probiotics

To our knowledge, commercial probiotics have been used in aquaculture since the early 80ties (Boyed et al., 1984) and until today (e.g. Zheng et al., 2017; Zhou et al., 2017; Interaminense et al., 2018; Pereira et al., 2018). However, recently, attention has focused on using host-microbiota as a probiotics source (e.g. Lazado et al., 2015; Interaminense et al., 2018; Li et al., 2018; Wang et al., 2018). They are naturally established within the host defense system (Gomez et al., 2013; Llewellyn et al., 2014), and revealed a large number of beneficial characteristics; such as intestinal enzymes and novel bioactive lipid sebastenoic acid (Lazado et al., 2012; Sanchez et al., 2012). This is important for fish farming, as fish are a rich source of probiotic strains that provide additional mechanisms against numerous infectious diseases (e.g. Spanggaard et al., 2000; Pandiyan et al., 2013; Carnevali et al., 2017). Host-related microbiota can be an alternative probiotic source within aquaculture, as terrestrial sources *per se* are mostly used (Lakshmi et al., 2013; Lazado et al., 2015). Today, most probiotic candidates are derived from the mucosal layers, the autochthonous bacteria, of aquatic animals (Balcázar et al., 2007; Newaj-Fyzul et al., 2007; Caipang et al., 2010; Lazado et al., 2010; Maeda et al., 2014; Lazado & Caipang 2014a; Tzuc et al., 2014). For example, probiotics isolated from the GI tract of channel catfish (*Ictalurus punctatus*) (Larsen et al., 2014), rainbow trout (*Oncorhynchus mykiss*) (Spanggaard et al., 2000; Araújo et al., 2015), Atlantic cod (*Gadus morhua*) (Dhanasiri et al., 2011; Fjellheim et al., 2007), and Atlantic salmon (*Salmo salar*) (Jöborn et al., 1999).

Two basic principles are generally applied as a guide for the use of host-associated bacteria as a probiotic (Lazado & Caipang, 2014a). The differences in physiological peculiarities and discrepancies of each host, as well as the considerable influences of various environmental factors make it hard to establish a probiotic candidate for global application (Lazado et al., 2015). For example, growth and bacteriocin production of *Leuconostoc mesenteroides* and *Lactobacillus curvatus* are affected by pH, temperature, and aquatic animal species (Mataragas et al., 2003). These parameters were reported to affect the adhesion ability of lactic acid bacteria (LAB) (Tuomola et al., 2001). Physiological variances between marine and terrestrial microorganisms exist, and impose differential responses to diverse environment (Morgan-Kiss et al., 2006; Lazado et al., 2015). Furthermore, a discrepancy exists in acquisition mechanism between marine and terrestrial microorganisms involved in inhibition of pathogen growth (Sandy & Butler, 2009), which is controlled by siderophore production; a mechanism of probiotics (Lazado et al., 2010; Ahmed & Holmström, 2014). The mode of action of bacterial iron acquisition includes siderophore-mediated transport, direct import through divalent metal transporters, or direct piracy from ironbound host proteins (Caza & Kronstad, 2013; Pokorzynski et al., 2017). Siderophores are low molecular weight substances with a high affinity for ferric iron, which are synthesized and secreted by bacteria in order to scavenge iron when the availability is limited. In Gram-negative bacteria, siderophore-bound iron is transported through cognate outer membrane receptors that require energy transduction via the TonB-ExbB-ExbD protein complex (Andrews et al., 2003; Ellermann & Arthur, 2017). The second mechanism depends on specific enzymatic hydrolysis of the siderophore, which serves to weaken its interactions with iron, and enable its liberation. In both Gram-negative and Gram-positive bacteria, ferrous iron is directly transported through cytoplasmic membrane permeases or ABC transporters (Kammler et al., 1993; Sabri *et al.,* 2006; Shapiro & Wencewicz, 2016). Some bacterial pathogens belonging to family Neisseriaceae, Pasteurellaceae and Moraxellaceae are also capable of utilizing host sources of iron by expressing outer membrane receptors that directly bind to host iron-binding proteins such as transferrin (Cornelissen, 2003; Parrow et al., 2013). The bottlenecks caused by the physio-chemical parameters on probiotic properties may be eliminated by using host-associated microorganisms as probiotics if these microorganisms are originally isolated from the environment where they were applied (Verschuere et al., 2000; Vadstein et al., 2013). Because the highest physiological activities of microorganisms are obtained in their natural habitats, we may presume that the ultimate benefits are achieved when they are applied in those conditions (Ibrahem, 2015).

Because existing knowledge is fragmentary, it is difficult to draw a solid scientific conclusion to whether host-associated microbiota are superior to terrestrial sources (Lazado et al., 2015). However, it is believed that the survival rate and function of host-associated probiotics are optimal when they are applied in the "natural" environment (Murall et al., 2017). The application of both host and non-host candidate probiotics in aquaculture represent promising future alternatives (Lazado et al., 2015). Additional beneficial effects are obtained when combining two or more microorganisms, providing that they do not inhibit each other. Previous findings have indicated that the functionality and efficacy of their administration are improved with the use of multi-strain probiotics (Timmerman et al., 2004; Mohapatra et al., 2014). In probiotics-mediated disease prevention, the best level of protection for a broad spectrum of fish pathogens can only be achieved through the use of multiple strains in dietary preparations (Merrifield et al., 2010). Interestingly, the use of host-associated probiotics addresses the above concerns, but also shows that host-microbiota have functions other than being a part of natural defense system, such as immunomodulation and nutrient conversion (Lazado et al., 2015; Montalban-Arques et al., 2015). This is bioprospecting in a lesser scale, with a sustainable core concept of improving the health and welfare of aquaculture animals, through the utilization of their own commensal microbes (Llewellyn et al., 2014; Lazado et al., 2015). Recent findings have revealed that the microbial community of fish intestines are a new source of probiotics, and offer a biosynthetic diversity for natural products discovery (Sanchez et al., 2012).

4. Host specificity

When discussing host-associated *vs.* terrestrial probiotics, host specificity is an important subject to mention. Adhesion of probiotic LAB was previously reported to be host specific, and Fuller (1989) stated, "*The attachment to epithelial cells is very host specific which means in practical terms that a strain which is suitable as pig probiotic may not be active in chick and other animals*". However, later studies have indicated that LAB originated from one host adhere to mucus of other species (e.g. Tuomola et al., 1999; Rinkinen et al., 2000, 2003; Nikoskelainen et al., 2001a,b). In a recent review by Li et al. (2018), adherence and colonization of microorganisms in the GI tract of fish was discussed. As *in vitro* and *ex vivo* studies suggested host specificity of LAB colonization in sturgeon (Askarian et al., 2011; Salma et al., 2011), Li et al. (2018) put forward the controversial hypothesis that host specificity of LAB does not occur in "*younger*" fish species, e.g. Atlantic cod, Atlantic salmon and turbot, while it occurs in older species, sturgeons; "*living fossil*". However, adhesion ability of LAB may be related to; adhesive and non-adhesive ability (Zhou et al., 2012), variation of mucin adhesion and cell surface characteristics depending on their isolation habitats indicated by Buntin et al. (2017), and hydrophobic properties (Grajek et al., 2016).

5. Mode of actions of probiotics

Probiotic microorganisms influence the immune responses of the host, as well as the interaction between these responses and their intestinal bacterial communities (Derrien & van Hylckama Vlieg, 2015; Fischbach & Segre, 2016). During the last decades, intensive studies on probiotics have shed new light on the importance of probiotics and their modes of action (Papadimitriou et al., 2015), and several modes of action have been proposed.

(I) Probiotics enhance feed utilization and weight gain promoters of aquatic animals (Hai, 2015b; Zorriehzahra et al., 2016). Probiotics improve the host's appetite and feed digestion by breaking down indigestible components, increase production of vitamins, and detoxify compounds in the diet (Giraffa et al., 2010; Zorriehzahra et al., 2016).

(II) Competitive exclusion of pathogens in the GI tract (Ringø et al., 2010a), by production of peroxide, bacteriocin, siderophore, and lysozyme enzymes (Yan et al., 2002). The physiological and immunological effects (Mohapatra et al., 2014; De et al., 2014) are considered to be two of the most important beneficial mechanisms of probiotic bacteria (Collado et al., 2010; Zorriehzahra et al., 2016).

(III) Improve the resistance of farmed aquatic animals against stress caused by several environmental hazards throughout the aquaculture activity (Nimrat et al., 2012; Zorriehzahra et al., 2016).

These modes of actions present the beneficial effects of probiotics in cultured aquatic animals. Nonetheless, future researches on the interaction between probiotics and the host, involving transcriptomic and proteomic analyses, are needed to understand of probiotic activity.

6. Host-associated probiotics and their applications in aquaculture

6.1 *Bacillus* sp.

Bacteria belonging to genus *Bacillus* has simple nutritional requirements, fast metabolic rate, ease to isolate and preserve, and secrete multiple bacteriocins make them good probiotic candidates (Moriarty, 1998; Ziaei-Nejad et al., 2006). Genus *Bacillus* is the most studied host-associated probiotic, among a wide variety of aquatic animals. To our knowledge, Yanbo and Zirong (2006) conducted the first study using host-associated probiotics in aquaculture. Their findings showed that *Bacillus* sp. supplementation diets significantly improved growth performance, survival rate, and feed conversion ratio; as well as protease and lipase activities in common carp (*Cyprinus carpio*) (Yanbo & Zirong, 2006). The authors suggested that these improvements were due to enhanced enzyme activities, resulting in improved diet digestibility; including proteins, starches, and lipid.

In channel catfish, dietary inclusion of *Bacillus* spp. isolated from oil or intestine, significantly increased channel catfish resistance towards *Edwardsiella ictaluri* and *Aeromonas hydrophila* (Ran et al., 2012). The improved diseases resistance was suggested to be attributable to a biologically meaningful discrepancy in the interactions between *Bacillus* strains and their respective host. Additionally, interactions may exist between host, pathogen, and probiotic bacteria that are influenced by environmental factors. Ran et al. (2012) suggested that more research is needed to clarify the complex interactions between the host, pathogen and the probiotic *Bacillus* strains, as well as how to improve the environment in order to obtain optimal biological control of disease.

A study with *Bacillus* sp. isolated from shrimp intestine, Cha et al. (2013) reported significant increase in growth performance, innate immune response, and disease resistance in olive flounder (*Paralichthys olivaceus*), to *Streptococcus iniae*. The authors speculated that the increase in growth performance of fish fed dietary *Bacillus* sp. was a result of improved diet utilization. The GI tract of fish are known to be very sensitive to nutrients, presenting immediate changes in digestive enzyme activity, leading to enhanced growth and well-being (Bolasina et al., 2006; Shan et al., 2008). Zhang et al. (2010) indicated that the growth improvement in sea cucumber (*Apostichopus japonicus*) fed a *Bacillus subtilis* supplemented diet was due to the increase in digestive activity via enhanced enzymatic activity. Previous probiotic studies suggested that supplementation increases the favorable microorganism in the host's gut, which in turn release exoenzymes that can improve feed utilization and health conditions (Vine et al., 2006; Yanbo & Zirong, 2006). These beneficial organisms secrete numerous proteases, which may play an important role in breakdown of peptide bonds of proteins, into monomers and free amino acids, which positively affect host's nutritional status (Macfarlane & Macfarlane, 2012).

Similarly, a significant increase in growth performance, immune response, and disease resistance were observed in orange-spotted grouper (*Epinephelus coioides*) larvae (Sun et al., 2013), rohu (*Labeo rohita*) (Ramesh et al., 2015), and striped catfish (*Pangasianodon hypophthalmus*) (Truong Thy et al., 2017) fed host-associated *Bacillus* sp. The authors suggested that further investigations are needed to evaluate the effect of probiotics on the immune function in fish larvae, and to estimate the duration of persistence of the *Bacillus* after discontinuation of probiotic supplementation.

There is limited information available regarding the effects of host-associated probiotics on the health and well-being of crustacean and mollusk. Nimrat et al. (2011) reported that giant tiger prawn (*Penaeus monodon*) fed *Bacillus* spp. isolated from shrimp intestines and pond sediment, presented significantly improved growth performance, and survival rate; as well as increasing the number of additional beneficial microbial probiotics. In mud crab (*Scylla paramamosain*), dietary administration of *Bacillus* spp. isolated from the crab's intestine significantly enhanced survival rate, respiratory burst activity, immune related genes expression, and resistance to *Vibrio parahaemolyticus* (Wu et al., 2014). A significant decrease in hemocytes mortality and increase resistance toward *Vibrio harveyi* were observed in Pacific oyster (*Crassostrea gigas*) fed *Bacillus* sp. isolated from Tunisian hypersaline (Fdhila et al., 2017). The significant improvement in growth performance within these findings may be due to the ability of *Bacillus* spp. to adhere to the intestinal mucosa of the host, allowing them to secrete a wide range of digestive enzymes; such as amylase, lipase, and protease; all of which facilitate feed utilization (Marzouk et al., 2008; Latorre et al., 2016). Moreover, *Bacillus* spp. has been reported to detoxify potentially harmful food components, and produce many essential vitamins in the B-complex group (particular vitamin B_{12} and biotin), which results in higher feed utilization and digestibility of feed components (Blain Kennedy et al., 1998; El-Haroun et al., 2006). Regarding the immunomodulatory effects of probiotics, it should be noted that adhesion and colonization of probiotics in the intestines of the host are necessary to enhance the immune response (Ausubel, 2005; Govender et al., 2014; Nishiyama et al., 2016; Li et al., 2018).

Probiotics interact with immune system via microbe associated molecular patterns (MAMPs), consisting of cell wall polysaccharides, peptidoglycans, lipoprotein anchors, and lipoteichoic acids (Hosoi et al., 2003). Cells or components within the immune system are then able to interact with MAMPs through pattern recognition receptor; such as Toll like receptors, C-type receptor, and nucleotide oligomerigation domain like receptors (Kleerebezem et al., 2010; Lebeer et al., 2010; Bron et al., 2012). Another critical feature of probiotics is their presence inside the host, in which they are potentially colonizing and replicating, which further serves to improve the host's health (Pandiyan et al., 2013). The colonization ability of probiotics within the GI tract of animals provides a necessary competition to indigenous microbiota (Hill, 1993). The ability to attach the gut surface is an important aspect of probiotics, which in turn is associated with mucous formation of the bacteria. These abilities are useful for protection against pathogen (Olsson et al., 1992), or immune stimulation (Salminen et al., 2007).

Other species within genus *Bacillus*; *Bacillus* OJ, *Bacillus amyloliquifaciens,* and *Bacillus aerophilus,* isolated from GI tracts of Pacific white shrimp (*Litopenaeus vannamei*), yellow fin bream (*Acanthopagrus latus*), and rohu significantly enhanced growth performance, immune response, and disease resistance of Pacific white shrimp (Li et al., 2009), Nile tilapia (*Oreochromis niloticus*) (Ridha & Azad, 2012), and rohu (Ramesh et al., 2017). More recently, Meidong et al. (2018) reported that *B. aerius* isolated from pla-mong (*Pangasius bocourti*) improved growth performance, immune responses, as well as resistance against *A. hydrophila*.

6.2 *Bacillus subtilis*

B. subtilis is one of the most studied species within genus *Bacillus*. Dietary administration of *B. subtilis* isolated from mrigal (*Cirrhinus mrigala*) significantly improved total serum protein, globulin content, antibody level, hematology and immune response, as well as disease resistance against *E. tarda* and *A. hydrophila* in rohu (Nayak et al., 2007; Kumar et al., 2008). In a study with grass carp (*Ctenopharyngodon idella*), Wu et al. (2012) revealed that dietary administration of *B. subtilis* isolated from grass carp significantly improved specific growth rate, feed conversion ratio, enzyme activity, and total bacteria counts in the GI tract of the fish. In a study using rainbow trout, reported Newaj-Fyzul et al. (2007) that dietary supplementation of *B. subtilis* isolated from rainbow trout intestines significantly enhanced respiratory burst, serum and gut lysozyme, peroxidase, phagocytic killing, and all α1-antiprotease activities. Furthermore, the study revealed a significant increase in lymphocyte population, as well as the resistance towards *A. hydrophila*. Likewise, the supplementation of *B. subtilis* isolated from intestines of sea cucumber, Japanese eel (*Anguilla japonica*), and pond water significantly enhanced the growth performance, immune response, enzyme activity, and disease resistance of sea cucumber, Japanese eel and Nile tilapia (Zhao et al., 2012; Lee et al., 2017; Liu et al., 2017). In Pacific white shrimp dietary inclusion of *B. subtilis* significantly increased survival rate, immune response, and resistance to *V. harveyi* (Liu et al., 2014). However, body crude lipid content significantly decreased in the shrimp fed *B. subtilis*, *vs*. the control diet. More recently, a *Bacillus* spp. revealing exoenzymes activities improved the host's growth performance, including weight gain and feed efficiency (Liu et al., 2017). *Bacillus* exoenzymes are very efficient at metabolizing a large variety of carbohydrates, lipids, and proteins (Liu et al., 2009), and dietary supplementation of bacilli may improve digestive enzyme activities (Han et al., 2015). It is widely accepted, that the level of digestive enzyme activity is a useful comparative indicator of the host's food utilization rate, digestive capacity, and growth performance (Ueberschär, 1995; Suzer et al., 2008).

Regarding immunomodulation and disease improvement, several mechanisms have been suggested, antimicrobial synthesis, pathogen competition, prevention of intestinal inflammation, and improvement of the GI tract microbiota (Suva et al., 2016). *B. subtilis* spores trigger specific humoral and cell-mediated immune responses (Amuguni & Tzipori, 2012). The interaction between *B. subtilis* spores and macrophages plays an important role in the development of both innate and adaptive immune responses of the host (Guo et al., 2016). Two studies have demonstrated that the inclusion of *B. subtilis* leads to successful macrophage activation. Suva et al. (2016) revealed that *B. subtilis* B10, *B. subtilis* BS02, and *B. subtilis* (*natto*) B4 spores might possess immunomodulatory activities, obtained through the induction of pro-inflammatory cytokines, which exert probiotic activities through activated macrophage functions. Commensal bacteria play an important role in the development of the gut-associated lymphoid tissue (GALT), and are important for both innate and adaptive immunity. *B. subtilis* promotes active lymphocyte proliferation within GI tract, due to their high metabolic activity. *Bacillus* activity is determined mainly by their ability to produce antibiotics; of which, *B. subtilis* is the most productive species. *Bacillus subtilis* devotes 4%–5% of its genome to antibiotic synthesis, and produces as many as 66 antibiotics. Each *Bacillus* antibiotic contains a different structure and spectrum of antimicrobial activity (Sorokulova, 2013).

6.3 *Bacillus cereus*

Few studies have used *B. cereus* as potential probiotic in fish and shrimp. Navin et al. (2014) indicated that the giant tiger prawn (*Penaeus monodon*) fed dietary inclusion of *B. cereus* isolated from shrimp’s intestines; significantly increase growth performance, feed conversion ratio, and immune response. Rengpipat et al. (2000) reported a similar improvement in immune response in shrimp, which they attributed to the presence of the surface antigens of *Bacillus* S11 and their metabolites, which serve as immunogens in the shrimp’s immune defense mechanisms. They also noted that the additional of *Bacillus* S11 cell wall peptidoglycan may trigger immune functions in shrimp. In a study using sea cucumber, Zhao et al. (2016) observed significant increases in phagocytosis, respiratory burst, and total nitric oxide synthase activities; as well as disease resistance to *Vibrio splendidus.* The dietary *B. cereus* isolated from the mud of sea cucumber culturing water bodies, while effective in the above ways, showed no changes in growth performance, total coelomocytes counts, acid phosphatase, or superoxide dismutase activities. This difference could be attributed to the specific *Bacillus* strains, the size and source of sea cucumbers, as well as experimental period and conditions (Zhao et al., 2016).

6.4 *Bacillus pumilus*

Bacillus pumilus is a *host-associated probiotic* of recently interest in the field of aquaculture. Dietary administration of *B. pumilus* or *B. pumilus* in combination with *B. clausii* isolated from fish hosts significant improved growth performance, immune response, and disease resistance of Nile tilapia *and* orange-spotted grouper (Sun et al., 2010; Srisapoome & Areechon, 2017). They concluded that the significant improvement in growth performance via *B. pumilus* diet was attributed to the absence of an antigenic stimulus provided by the pathogenic bacteria could reduce a number of immune cells. This condition may create the efficient absorption and utilization of nutrients in the intestines (Sun et al., 2010). Significant enhancement of fish health and disease resistance may be credited to the increase in none-specific immunity by enhancing phagocytic activity, the number of vital leukocytes, and superoxide anion production. In theory, *B. pumilus* provides high anti-spore IgG titers, pro-inflammatory tumor necrosis factor, and a bacteriocin-like activity against other *Bacillus* (Duc et al., 2004); as well as complement activity (Sun et al., 2010). These abilities may effectively elevate the survival rate of experimental fish fed *B. pumilus* (Aly et al., 2008).

6.5 *Bacillus licheniformis*

B. licheniformis is another efficient *host-associated probiotic* in aquaculture. Grass carp fed dietary *B. licheniformis* and *B. subtilis* isolated from the grass carp pond, significantly increased globulin level, IgM, lysozyme, and complement activities; as well as myeloperoxidase content, superoxide anion production, total antioxidant activity, glutathione, and anti-superoxide anion free radical (Weifen et al., 2012). The improvement in fish immunity may be due to supplementation of *Bacillus*, which improves water quality, resulting in better living condition for fish (Lalloo et al., 2007; Borges et al., 2008; Wang et al., 2008). The addition of probiotic bacteria to the water environment can decrease harmful microorganisms, act as a food source for zooplanktons, and stimulate remineralization of macronutrients and micronutrients that boost phytoplankton growth, and thereby enhance the oxygen level (Verschuere et al., 2000). *Bacillus* species reduces the abundance of pathogenic *Vibrio* bacteria in *in vitro* test and improves water quality through the reduction of toxic NH_4^+ and NO_2^-, maintaining a neutral pH (Nimrat et al., 2012). Additionally, *Bacillus* produce antimicrobial compounds (Rengpipat et al., 1998; Ringø et al., 2007; Nayak, 2010; Nandi et al., 2018). *Bacillus* preparations, added to the water, 10^8 CFU m^3, increased serum immunoglobulin levels, non-specific immune parameters and the antioxidant ability of grass carp, but by adding *Bacillus* preparations into the water and feed, 10^8 CFU g^{-1}, significantly improved immune effects were revealed (Weifen et al., 2012). Adding probiotics in both water and feed may provide better opportunities for the colonization of probiotics in the fish intestine, thereby enabling them to compete with pathogens for nutrients, and/or to inhibit the growth of pathogens; thus altering the prophylactic use of chemicals, antibiotics, and biocides (Decamp et al., 2008; Ma et al., 2009). The approach by adding probiotics to water and feed is better to use in saltwater as the environment is saltier, the fish loses water passively, and the fish has to drink. The noticeable increase in antioxidant enzyme activity may be due to that *Bacillus* act as antigen, which can stimulate the body's antioxidant enzyme system and increase the amount of antioxidants (Weifen et al., 2012; Wang et al., 2017). These antioxidant enzymes effectively remove excessive free radicals produced by a high metabolism and adverse environmental stress; as well as regulate of the body's free radical balance, and repair damages to tissues and organs (e.g. Harris, 1992; Gill et al., 2010). Recently, Gobi et al. (2018) displayed that dietary administration of *B. licheniformis* significantly improved growth performance, mucus and serum immune parameters, antioxidant enzyme activity, and resistance to *A. hydrophila* in tilapia. It is known that increase in fish body weight gain by feeding fish probiotic supplemented diets, could be contributed to the increase in digestive enzyme activity, increase in appetite, increase in the production of vitamin, breakdown of indigestible components, as well as possible improvement of intestinal morphology (Irianto & Austin, 2002).

There have been numerous investigations on the immunomodulatory effect of probiotics on different immune cells to enhance immune responses (e.g. Nayak et al., 2010; Das et al., 2013; Sangma & Kamilya, 2015; Gobi et al., 2018). Mucus and serum protein were significantly higher in rohu fed a *B. subtilis* supplemented diet, catla (*Catla catla*) fed a diet added *B. amyloliquifaciens*, and catla fed *B. subtilis* (Nayak et al., 2010; Das et al., 2013; Sangma & Kamilya, 2015). Similarly, Gobi et al. (2018) revealed that serum protein and mucus protein were significantly higher in tilapia (*Oreochromis mossambicus*) fed *B. licheniformis* Dahb1 supplemented diets. Serum protein and mucus protein associated with agglutinins, lectins, lysozyme, immunoglobulins are considered as important proteins involved in the defense mechanism (Alexander & Ingram, 1992; Esteban, 2012). Gobi et al. (2018) suggested that tilapia fed diets containing *B. licheniformis* Dahb1 or other probiotics increased the level of these proteins, and subsequently increased serum and mucus protein concentration.

6.6 Lactic acid bacteria

The host-associated lactobacilli have gained much attention in aquaculture, for review see the comprehensive review of Ringø et al. (2018). Harikrishnan et al. (2010) reported that kelp grouper (*Epinephelus bruneus*) fed dietary *Lactobacillus sakei* isolated from olive flounder intestine significantly increased macrophage phagocytic, peroxidase, serum lysozyme activities, and total protein levels; as well as a resistance to *S. iniae* and *S. parauberis.* In addition, Pacific red snapper (*Lutjanus peru*) fed *Lb. sakei* isolated from the mucus of spotted sand bass (*Paralabrax maculatofaciatus*) significantly promoted haemoglobin, myeloperoxidase, lysozyme, and total antiproteases activities; as well as IgM, serum antioxidant capabilities, and vacuoles inside the enterocytes (Reyes-Becerril et al., 2014). Enhanced fish growth following feeding of *Lb. sakei* may be due to the improvement of nutrient digestibility and/or to the alteration of the intestinal microbiota and immunostimulation (Reyes-Becerril et al., 2012). The chemical composition of microorganisms includes different polysaccharides that may have potential prebiotics in the host's intestine (Ringø et al., 2010b). Both bifidobacteria and lactobacilli are capable of utilizing these oligosaccharides, and increase the number of beneficial bacteria in host's gut. Further benefits of dietary supplemented oligosaccharides; include improved feed efficiency, enhanced growth, and increased digestive enzyme activities. Furthermore, they seem able to modulate immune responses and preserve the integrity of the intestinal wall (Xu et al., 2009; Dimitroglou et al., 2010).

Lactobacillus plantarum has also gained popularity in fish and shellfish farming. Kongnum & Hongpattarakere (2012) revealed that *Lactobacillus plantarum* isolated from the shrimp intestines significantly improved relative growth rate, feed conversion ratio, survival rate, and hemocytes count as well as disease resistance to *V. harveyi* in Pacific white shrimp. Similarly, significant increases in growth performance, feed utilization efficiency, survival rate, enzyme activity, immune response, and disease resistance to *A. hydrophila* were observed in rohu (Giri et al., 2013); and swimming crab (*Portunus pelagicus*) (Talpur et al., 2013). More recently, the dietary supplementation of *Lb. plantarum, Weissella confuse, Lactococcus lactic,* and *Enterococcus faecalis* were investigated (Li et al., 2018b). The bacteria were isolated from the intestines of flathead grey mullet (*Mugil cephalus*), rockfish (*Sebastes schlegeli*), fat greenling (*Hexagrammos otakii*), and söhachi (*Cleisthenes herzensteini*) and significantly stimulated growth performance, disease resistance against *V. splendidu*s, alkaline phosphatase, acid phosphatase, super oxide dismutase, lysozyme activity, and up-regulated heat shock proteins genes of juvenile sea cucumber. The elevated of growth rate of aquatic animals may be related to the effects of LAB actions on competitive exclusion of pathogenic bacteria, supplying hydrolytic enzymes, and/or by supplying fatty acid and vitamins (Huang et al., 2014; Hai, 2015b). Regarding the immunostimulatory effects of *Lb. plantarum,* it was reported that lactobacilli could elicit innate and adaptive immune responses in the host via binding to the pattern recognition receptors (PRR) expressed on immune cells and many other tissues, including the intestinal epithelium. PRR recognize the conserved molecular structures known as microbe-associated molecular patterns, which induce the production of cytokines, chemokines, and other innate effectors (Abreu, 2010; Kawai & Akira, 2010; Wells et al., 2010). In addition to lactobacilli, are several other genera of LAB used as probiotics in aquaculture, *Enterococcus, Lactococcus,* and *Weissella. Enterococcus faecium* isolated from the intestine of flathead grey mullet significantly boosted nitroblue tetrazolium assay and common carp resistance to *A. hydrophila* (Gopalakannan & Arul, 2011). The authors suggested that the reason of the noticed results might be the extracellular products of probiotic bacteria, such as bacteriocin- and nisin-like compounds, which induce the immune system of common carp. Additionally, there are several mechanisms through which probiotic bacteria can induce bacterial antagonism, by producing antimicrobial agents, like antibiotics, antimicrobial peptides (bacteriocins), siderophore substances, or hydrogen peroxide (e.g. Sugita et al., 1998; Ringø et al., 2018). Like many probiotics, *E. faecium* produce bacteriocin, which creates a pore in the cell membrane of pathogens, which leads to the efflux of K^+ ions, resulting in cell death (Satish & Arul, 2009). In a study with grouper, Sun et al. (2012) reported that dietary supplementation of *E. faecium* and *Lactococcus lactic*, originating from the gut of orange-spotted grouper, significantly increased feed utilization, hepatopancreatic protease activities, complement component-3, and serum lysozyme activities; however, no change in phagocytic, serum superoxide dismutase activities, IgM, or complement component-4 were observed. Similarly, significant improvements in growth performance, innate immune response, up-regulation of lysozyme genes, and disease resistance to *Streptococcosis* were observed in kurumar shrimp (*Marsupenaeus japonicus*) and olive flounder, fed host-associated *Lactococcus lactic* as a probiotic (Maeda et al., 2014; Nguyen et al., 2017). Allameh et al. (2014) isolated an *E. faecalis* from intestine of snakehead fish (*Channa striatus*) and revealed significantly improved resistance of snakehead fish against *A. hydrophila* when the *E. faecalis* was included in the diet. More recently, Mouriño et al. (2016) reported that hybrid surubim catfish (*Pseudoplatystoma reticulatum* ♀ × *P. corruscans* ♂), fed *Weissella cibaria* isolated from its foregut intestine, showed a significant increased red blood cell count. However, no significant difference occurred in white blood cells, total thrombocyte count, haematocrit percentage, basophils and other leukocytes; as well as glucose levels between supplemented diets and control.

6.7 Other host-associated probiotics

Aeromonas sobria has been used as a potential probiotic in aquaculture (Brunt & Austin, 2005). The authors suggested that dietary administration of *A. sobria* isolated from GI tract of rainbow trout significantly enhanced appetite, leukocytes count, phagocytic and respiratory burst activities; as well as resistance to *Lactococcus garvieae* and *S. iniae*. The mode of action of *A. sobria* involves the stimulation of cellular immunity, which directly increases the number of leucocytes, and enhances phagocytic and respiratory burst activities. It remains speculative, exactly how *A. sobria* stimulates this activity when used as a feed supplement (Brunt & Austin, 2005).

Senegalese sole (*Solea senegalensis*) fed diet supplemented with two *Shewanella*, Pdp11 and Pdp13 isolated from gilthead sea bream skin, significantly increased growth and nutrient utilization, proximate composition, and alkaline phosphatase of juvenile sole (Sáenz et al., 2009). Sharifuzzaman & Austin (2009) conducted an experiment with the use of *Kocuria* SM1isolated from the digestive tract of rainbow trout. Fish fed dietary *Kocuria* SM1 at concentration of 10^8 cells g^{-1} for four weeks showed significantly enhanced phagocytic, peroxidase, and serum lysozyme activities. In a study with rainbow trout, LaPatra et al. (2014) revealed that feeding host-associated *Enterobacter* sp. significantly increased survival rate, antibody titers, and resistance to *Flavobacterium psychrophilum*. Similarly, significant increase were noticed on growth performance, tolerance to crowding stress, microbiota, enzyme activities, innate immune response, relative immune gene expressions, and disease resistance in fish and shellfish fed *Shewanella putrefaciens*, *Psychrobacter namhaensis, Pseudoalteromonas*, and *Clostridium butyricum* host- associated probiotics (Tapia-Paniagua et al., 2014; Makled et al., 2017; Offret et al., 2018; Sumon et al., 2018). The significant increase in growth performance and health status of fish, as well as disease resistance within above studies are possibly due to the increase in digestive enzyme activities, absorptive capacities of the intestine, innate immune, relative immune gene expressions, and modulate GI tract microbiota.

In the pioneer review devoted to "*Probiotics in man and animals*", Fuller (1989) wrote, "*Probiotic preparations may consist of single strains or may contain any number up to eight strains*". However, most probiotic studies carried out in aquaculture since the early 1990ties and until today have used single administration, but during the last decade, supplementation of multiple probiotics in the diets to aquatic animals has gained interest (e.g. Mohapatra et al., 2011; Ibrahem, 2015; Zorriehzahra et al., 2016). The advantage of multiple-strain preparations is; they are active against wider range of conditions and species.

Dietary inclusion of *Enterobacter cloacae* and *Bacillus mojavensis*, singular or combined, significantly improved growth performance, cellular immunity, and disease resistance of rainbow trout (Capkin & Altinok, 2009). These improvements may be due to the probiotic effects of these two microorganisms. Probiotics stimulate the digestive processes through the proliferation of a favorable microbiota population, enhancing microbial enzyme activity, improving the intestinal microbial balance; and, consequently, improving the digestibility, absorption of food, and feed utilization (El-Haroun et al., 2006; Capkin & Altinok, 2009). The authors indicated that the putative probiotic bacteria isolated from intestines of rainbow trout possess antibacterial abilities. Presence of such intestinal bacteria in the GI tract can protect fish against infections caused by pathogenic bacteria (Capkin & Altinok 2009). The mode of action of *Enterobacter* and *B. mojavensis* is to stimulate cellular immunity, specifically due to an increased number of leucocytes. *E. cloacae* are listed under the same family as *Y. ruckeri*, Enterobacteriaceae. This strain may not only competitively exclude *Y. ruckeri*, but also present an appearance likely to trigger higher immune reactions than that of an unrelated *Bacillus* (Capkin & Altinok, 2009). Similarly, the combination of three probiotics; *Bacillus coagulans, Rhodoseudomonas palustris,* and *Lactobacillus acidophilus* isolated from intestines of common carp and grass carp significantly increased weight gain, final weight, and digestive enzyme activity of grass carp (Wang, 2011). Chi et al. (2014) revealed that the dietary supplementation of *Aeromonas veronii, Vibrio lentus,* and *Flavobacterium sasangense* derived from GI tract of common carp significantly boosted total serum protein, albumin and globulin levels, innate immune response, and expression of 1L-1b and TNF-α in common carp. Similar results improving growth performance, digestive enzyme activities, stress indicators, immune response, relative immune gene expressions, modulation of gut microbiota composition, and disease resistance were observed in rainbow trout fed *Kocuria* SM1 and *Rhodococcus* SM2 (Sharifuzzaman et al., 2014), in grass carp fed *Shewanella xiamenensis* and *A. veronii* (Wu et al., 2015), in sea cucumber fed *Bacillus cereus*, *B. cereus,* and *Paracoccus marcusii* (Yang et al., 2015), in Malaysian mahseer (*Tor tambroides*) fed *Bacillus* sp. and *Alcaligenes* sp. or *Bacillus* sp., *Alcaligenes* sp. and *Shewanella* sp. (Asaduzzaman et al., 2018a, b). In a study using Pacific white shrimp, dietary administration of host-associated *Shewanella haliotis, B. cereus,* and *Aeromonas bivalvium* significantly stimulated respiratory burst, superoxide dismutase, respiratory burst activity, acid phosphatase activities, and up-regulated prophenoloxidase and β-glucan-binding protein genes, as well as resistance to *V. harveyi* (Hao et al., 2014). In recent studies with Pacific white shrimp fed host-associated probiotics *Rhodobacter sphaeroides* and *Afifella marina* or *B. subtilis* and *S. algae* isolated from ponds or its GI tract; significantly improvements in water quality, growth performance, resistance to acute hepatopancreatic necrosis disease (AHPND), and control *Vibrio* in shrimp hepatopancreas were observed (Chumpol et al., 2017; Interaminense et al., 2018). As with other host-associated probiotics, significant improvements in growth performance, immune response, and disease resistance of fish may be due to the increase in digestive enzyme activities, absorptive capacities of the intestine, innate immune and relative immune gene expressions, modulation of the GI tract microbiota, and production of antibacterial substances (Van Doan et al., 2018). Additionally, a recent study reported that growth performance improvement of Malaysian mahseer was governed primary by muscle fibres hypertrophy and up-regulated growth related (*GH* and *IGF1*) gene expression (Asaduzzaman et al., 2018b).

In contrast, Allameh et al. (2016) revealed that inclusion of individual LAB strains in the diet resulted in significantly improved growth performances of Javanese carps compared to fish fed a diet supplemented a LAB mixture. Dietary inclusion *E. faecalis* at 10^7 cfu g^{-1} revealed higher growth performance compared to other treatments. Additionally, the population levels of LAB in the fish intestine significantly increased, while the levels of Gram-negative bacteria significantly decreased *vs*. the control.

7. Conclusions and future applications of probiotic in aquaculture

The present review addressed whether or not host-associated probiotics *vs*. probiotics obtained from other sources and commercial probiotics are more suitable to use in aquaculture. Although some studies have revealed beneficial effects of host-associated probiotics on performance, immune responses and disease resistance of aquatic organisms, the observed effects were species-specific. Therefore, it is necessary to carry out additional studies where both host-associated probiotics and probiotics obtained from other sources are used in the same study, and to determine optimum inclusion levels for host-associated probiotics. In order, to evaluate *in vivo* adherence and colonization of the host-associated probiotic strains within the complex microbial ecosystem of the intestine, detection of green fluorescence protein (GFP) tagged strains or fluorescence *in situ* hybridization (FISH) targeting 16S rRNA to identify the probiotics on the mucus surface must be carried out. Furthermore, mucus associated (autochthonous) microbiome must be investigated by next-generation sequencing (NGS), transcriptomic or proteomic profiling, and not the allochthonous microbiome; mostly investigated *per sc*. In addition, we recommend that gnotobiotic approaches are used in future studies, as the gnotobiotic approaches have been reported to have important roles to understand the function of gut microbiota on numerous biological processes of the host. Moreover, data is needed to understand the mechanisms by which the immune system of the intestinal mucosa discriminates between pathogenic, probiotics and commensal microorganisms. In summary, the present study revealed higher effectiveness of host-associated probiotics compared probiotics obtained from other sources, but increased attention towards isolation, optimum inclusion level and administration of host-associated probiotics in aquaculture is needed.

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