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REVIEW ARTICLE

The use of probiotics in aquaculture

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Summary

This study aims to present comprehensive notes for the use of probiotics in aquaculture. Probiotics have been proven to be positive promoters of aquatic animal growth, survival and health. In aquaculture, intestines, gills, the skin mucus of aquatic animals, and habitats or even culture collections and commercial products, can be sources for acquiring appropriate probiotics, which have been identified as bacteria (Gram-positive and Gram-negative) and nonbacteria (bacteriophages, microalgae and yeasts). While a bacterium is a pathogen to one aquatic animal, it can bring benefits to another fish species; a screening process plays a significant role in making a probiotic species specific. The administration of probiotics varies from oral/water routine to feed additives, of which the latter is commonly used in aquaculture. Probiotic applications can be either mono or multiple strains, or even in combination with prebiotic, immunostimulants such as synbiotics and synbiotism, and in live or dead forms. Encapsulating probiotics with live feed is a suitable approach to convey probiotics to aquatic animals. Dosage and duration of time are significant factors in providing desired results. Several modes of actions of probiotics are presented, while some others are not fully understood. Suggestions for further studies on the effects of probiotics in aquaculture are proposed.

Introduction

Aquaculture is viewed as an important food security sector for a growing global human population, and has rapidly developed due to intensified culture methods. An indiscriminate use of chemical additives and veterinary medicines as preventative and curative measures for diseases has resulted in antimicrobial resistance among pathogenic bacteria, and degraded environmental conditions (Bachère 2000). Consequently, serious loss because of the spread of diseases has been increasingly recorded. This is a significant constraint on aquaculture production and trade, and negatively affects economic development in many countries. Several alternative methods have been considered to improve the quality and sustainability of aquaculture production (Li *et al.* 2006). Of those methods, probiotics have been shown to have an important role in aquaculture (Skjermo and Vadstein 1999).

Although probiotics offer a promising alternative to chemicals and antibiotics in aquatic animals (Rekiel *et al.* 2007), and as an aid in the protection of aquacultured species, the ways that probiotics are used in aquaculture need to be considered to avoid producing negative results. As aquatic animals interact with a diverse range of micro-organisms within animals and their habitat, a screening probiotic process for particular fish species plays a vital role to make them species specific for obtaining desired results, in which *in vitro* and *in vivo* tests need to be carried out carefully. In addition, choosing appropriate administration methods leads to the creation of favourable conditions, in which probiotics are able to perform well. Probiotic administrations have been widely applied via water routine or feed additives (Moriarty 1998; Skjermo and Vadstein 1999) with either single or a combination of probiotics or even a mixture with prebiotics or other immunostimulants (Hai and Fotedar 2009). A better understanding of the modes of action may lead to effective and appropriate applications of probiotics into aquatic systems. Unfortunately, the mode of action is not always addressed.

This study aims to provide useful insights for the use of probiotics in aquaculture, offering a critical evaluation from a screen of potential probiotics of their effectiveness to the hosts. Moreover, some doubts on the results are also raised, while some suggestions for future studies are proposed.

Definition

As aquaculture is facing the problem of massive loss caused by diseases, there are a range of approaches available to protect farmed aquatic animals against the effect of pathogens. Of these approaches, probiotics have become widely used for the control of disease. The original definition of probiotics as organisms and substances contributing to intestinal microbial balance was provided by Parker (1974). As new findings emerged, several definitions of probiotics have been modified and proposed. Probiotics are cultured products or live microbial feed supplements, which beneficially affect the host by improving the intestinal (microbial) balance (Fuller 1989). A probiotic is a mono or mixed culture of live micro-organisms to improve the properties of the indigenous microflora (Havenaar *et al.* 1992). Probiotics are defined as live intestinal bacteria that promote the viability of the host (Skjermo and Vadstein 1999). Probiotics can also be defined as microbial cells administered through the gastrointestinal (GI) tract to improve the health of the hosts (Gatesoupe 1999).

As the intestinal microbiota in aquatic animals constantly interacts with the environment and the host functions, a probiotic is defined as a live microbial adjunct which provides beneficial effects viz., (i) modifying the host-associated or ambient microbial community, (ii) improving the use of feed or enhancing its nutritional value, enhancing the response of the host towards diseases, or (iii) improving the quality of its ambient environment (Verschuere *et al.* 2000). The definition of probiotics was as 'live micro-organisms which when administered in adequate amounts confer a health benefit to the host' (FAO/WHO 2001). A probiotic can be seen as a live, dead or component of a microbial cell, which is administered via the feed or to the rearing water, benefiting the host by improving disease resistance, health status, growth performance, feed utilization, stress response or general vigour, which is achieved via improving the hosts microbial balance or the microbial balance of the ambient environment (Merrifield *et al.* 2010b).

In addition, probiotics have been widely used in human and veterinary medicine. They are mainly lactic acid bacteria, putative *Lactobacillus* spp. (Fuller 1989). The use of probiotics in aquaculture includes bacteria and nonbacteria, with application via water routine and feed supplement. Probiotics provide benefits to the hosts viz., improving the host growth (Kumar *et al.* 2006; Boonthai *et al.* 2011; Silva *et al.* 2013), reducing the incidence of diseases (Irianto and Austin 2002b; Newaj-Fyzul *et al.* 2007; Silva *et al.* 2013), and requiring less chemotherapy (Irianto and Austin 2002a; Azad and Al-Mazouk 2008; Hai *et al.* 2009a). Moreover, probiotics can perform well in various aquatic environments: freshwater (Rahiman *et al.* 2010), brackish water and sea water (Vijayan *et al.* 2006). Generally, probiotics are live and/or dead microbial feed supplements or water additives in the form of mono, multiple strains or in combination with prebiotics or other immunostimulants, which are administered to improve the rearing water quality, to enhance the physiological and immune responses of aquatic animals, and to reduce the use of chemicals and antibiotics in aquaculture.

Screening potential probiotics

Potential probiotics may be commonly obtained from various sources viz. the GI tracts of aquatic animals (Jöborn *et al.* 1997, 1999; Newaj-Fyzul *et al.* 2007; Leyva-Madrigal *et al.* 2011; Luis-Villasenor *et al.* 2011; Cao *et al.* 2012; Del'duca *et al.* 2013; Sun *et al.* 2013; Beck *et al.* 2015; Ramesh *et al.* 2015), and fish mucus (Smith and Davey 1993; Tapia-Paniagua *et al.* 2012). Particularly they are the collected cultures (Hjelm *et al.* 2004; Thompson *et al.* 2010) and commercial products (Chang and Liu 2002; Hai *et al.* 2007; Suzer *et al.* 2008), in which the latter is a controversial issue as they are available in markets, but whether they are appropriate probiotics for other specific aquatic animals, needs to be investigated. The sources can also be the aquatic environment such as water or sediment (Garriques and Arevalo 1995; Hai *et al.* 2007; Preetha *et al.* 2007; Del'duca *et al.* 2013), or isolated from microbial bioflakes (Ferreira *et al.* 2015).

Desirable characteristics for the selection of potential probiotics include (i) no harm to the host; (ii) acceptance by the host through ingestion, and colonization and proliferation within the host; (iii) ability to reach target organs where they can work; and (iv) no virulent resistance or antibacterial resistance genes (Verschuere *et al.* 2000; Kesarcodi-Watson *et al.* 2008). The reasons for selecting potential probiotics are based on their inhibitory activity against target pathogens *in vitro* (Jöborn *et al.* 1997, 1999; Bourouni *et al.* 2007; Cao *et al.* 2012). They have to be evaluated for safety (Verschuere *et al.* 2000), or for pathogenicity (Chythanya *et al.* 2002) to the hosts. Probiotics should be tested for their inhibitory activity against targeted pathogens (Vijayan *et al.* 2006; Hai *et al.* 2007) or for their protection of hosts when challenged with pathogens (Irianto and Austin 2002b; Vaseeharan *et al.* 2004). The application of quorum sensing shows that potential probiotics can degrade acylated homoserine lactone molecules produced by fish pathogens (De Kievit and Iglewski 2000; Defoirdt *et al.* 2004; Tinh *et al.* 2007a; Chu *et al.* 2011), particularly in *Vibrio harveyi* (Defoirdt *et al.* 2004; Tinh *et al.* 2007b) and *Pseudomonas aeruginosa* (De Kievit and Iglewski 2000).

As new findings emerged through practice over the last decades, more criteria have been added to the list for selecting potential probiotics in aquaculture. Generally, the potential probiotic properties include (i) to be harmless to the host, (ii) to be accepted by the host, (iii) to reach a target place to perform, (iv) to work *in vivo* as opposed to *in vitro* findings, and (v) to contain no virulent resistance genes (Kesarcodi-Watson *et al.* 2008). Merrifield *et al.* (2010b) extended that list with characteristics, of which some are essential and some considered as merely favourable. It is unlikely a candidate will be found to fulfil all of these characteristics. Theoretically, the candidate probiotic that fulfils more of these characteristics than others shall be considered an appropriate probiotic. Some *in vivo* tests should be carried out (Verschuere *et al.* 2000) before application on a large scale. In screening processes, it should be noted that not all probiotic activities are displayed on agar plates, and positive results *in vitro* sometimes fail to determine an *in vivo* effect (Kesarcodi-Watson *et al.* 2008).

Probiotic components

Probiotics have been widely used in human and veterinary medicine (Khuntia and Chaudhary 2002). Probiotics are common bacteria, For example, lactic-acid producing bacteria are used widely in terrestrial animals (Lauzon *et al.* 2008), while a wide range of micro-organisms is employed in aquaculture, in which both Gram-positive and Gram-negative bacteria are administered effectively. Other nonbacteria candidates such as bacteriophages, microalgae and yeasts are explored commonly as probiotics for use in aquaculture.

A diverse range of Gram-positive bacteria is commonly used worldwide as probiotics. The wide applications belong to endospore-forming members of *Bacillus* genera (Hong *et al.* 2005), in which *Bacillus subtilis* is commonly used in aquaculture. Other Gram-positive bacteria can be seen in Table 1. A wide variety of Gram-negative bacteria also play a role as putative probiotics in aquaculture. Although Gram-negative bacteria are not commonly administered in aquaculture, a long list of diverse species can also be seen in Table 1.

Other nonbacteria candidates are also employed as probiotics in aquaculture, of which bacteriophages, microalgae and yeasts are explored. Bacteriophages from two families of Myoviridae and Podoviridae enhanced ayu fish (*Plecoglossus altivelis*) to protect against *Pseudomonas plecoglossicida* and improved water quality with fewer bacterial pathogens (Park *et al.* 2000). Controversially, as phage therapy was considered as an alternative to the use of antibiotics in aquaculture, lysogenic phages have been shown to have the ability to transform nonvirulent bacterial strains in to virulent strains (Rao and Lalitha 2015).

Various microalgae viz., *Dunaliella salina*, *Dunaliella tertiolecta*, *Isochrysis galbana*, *Phaedactylum tricornutum* and *Tetraselmis suecica* have improved the growth and survival, and enhanced the health of aquatic animals (Nass *et al.* 1992; Reitan *et al.* 1997; Cahu *et al.* 1998; Supamattaya *et al.* 2005; Marques *et al.* 2006). *Dunaliella tertiolecta* enhanced the protection of gnotobiotic *Artemia* against *Vibrio campbellii* and *Vibrio proteolyticus* (Marques *et al.* 2006). *Tetraselmis suecica* reduced bacterial diseases for penaeids and salmonids (Austin and Day 1990). Microalgae *Chaetoceros* spp., *Tetraselmis* sp., *Phaeodactylum* sp. inhibited to *Vibrio* spp., and were extensively used as probiotics in aquaculture (Naviner *et al.* 1999). Diatom, *Haslea karadagensis* produced a marennine-like pigment, which highlights antibacterial, antifungal and antiviral activities, therefore, they are used as a prophylactic treatment based on microalgal diets for bivalves (Gastineau *et al.* 2012).

Several yeasts have been proven to provide benefits to aquatic animals. *Saccharomyces cerevisiae* has been recognized to have potential as a substitute for live feed in the production of clown fish, *Amphiprion percula* (Gunasundari *et al.* 2013), catla, *Catla catla* (Mohanty *et al.* 1996), hybrid striped bass, *Morone chrysops* × *M. saxatilis* (Li and Gatlin 2004, 2005) and Japanese flounder, *Paralichthys olivaceus* (Taoka *et al.* 2006a), and Nile tilapia, *Oreochromis niloticus* (Lara-Flores *et al.* 2003). *Saccharomyces cerevisiae* was used as a probiotic for Nile tilapia (Lara-Flores *et al.* 2003; Meurer *et al.* 2006) and common carp, *Cyprinus carpio*, (Faramarzi *et al.* 2011). *Saccharomyces cerevisiae* improved resistance to vibriosis of juvenile penaeids (Scholz *et al.* 1999). Marine yeast, *Yarrowia lipolytica*, improved the survival and growth of pearl oyster, *Pinctada mazatlanica* (Aguilar-Macias *et al.* 2010). Live yeast *Debaryomyces hansenii* enhanced the growth performance of sea bass *Dicentrarchus labrax* larvae (Tovar-Ramírez *et al.* 2010).

Administration methods

Water and feed additives

Probiotics administration varies from direct oral/water routine or feed additives, in which the former is considered

Table 1 A diverse range of Gram-positive and Gram-negative bacteria can be used as probiotics

Gram-positive bacteria	References	Gram-negative bacteria	References
Arthrobacter sp.	Li *et al.* (2008)	*Aeromonas* spp.	Gibson *et al.* (1998); Irianto and Austin (2002a,b)
Bacillus subtilis	Vaseeharan and Ramasamy (2003); Salinas *et al.* (2005); Newaj-Fyzul *et al.* (2007); Zokaeifar *et al.* (2012); Del'duca *et al.* (2013)	*Agarivorans* sp.	Silva-Aciares *et al.* (2011)
Brevibacillus sp.	Mahdhi *et al.* (2012)	*Alteromonas* spp.	Douillet and Langdon (1994); Kesarcodi-Watson *et al.* (2010, 2012b)
Brochothrix sp.	Pieters *et al.* (2008)	*Bdellovibrios* spp.	Cao *et al.* (2012)
Clostridium sp.	Sakai *et al.* (1995); Pan *et al.* (2008a,b)	*Burkholderia* sp.	Aguilar-Macias *et al.* (2010); Granados-Amores *et al.* (2012)
Carnobacterium spp.	Kim and Austin (2006)	*Enterobacter* spp.	Burbank *et al.* (2011)
Enterococcus spp.	Swain *et al.* (2009); Del'duca *et al.* (2013)	*Neptunomonas* sp.	Kesarcodi-Watson *et al.* (2010)
Kocuria sp.	Sharifuzzaman and Austin (2010a)	*Phaeobacter* spp.	Kesarcodi-Watson *et al.* (2012b); D'alvise *et al.* (2013)
Lactobacillus spp.	Salinas *et al.* (2005); Aly *et al.* (2008c); Vendrell *et al.* (2008); Aguilar-Macias *et al.* (2010)	*Pseudoalteromonas* spp.	Fjellheim *et al.* (2010); Kesarcodi-Watson *et al.* (2012b)
Lactococcus spp.	Balcázar *et al.* (2007b); Del'duca *et al.* (2013)	*Pseudomonas* spp.	Hai *et al.* (2009a); Aguilar-Macias *et al.* (2010); Granados-Amores *et al.* (2012)
Leuconostoc spp.	Balcázar *et al.* (2007b); Vendrell *et al.* (2008)	*Rhodopseudomonas* sp.	Wang and Gu (2010); Zhou *et al.* (2010)
Microbacterium sp.	Fjellheim *et al.* (2010)	*Roseobacter* spp.	Ruiz-Ponte *et al.* (1999); Planas *et al.* (2006)
Micrococcus spp.	Irianto and Austin (2002b); Jayaprakash *et al.* (2005); Abd El-Rhman *et al.* (2009)	*Shewanella* spp.	De La Banda *et al.* (2012); Tapia-Paniagua *et al.* (2012); Jiang *et al.* (2013)
Pediococcus spp.	Aubin *et al.* (2005); Standen *et al.* (2013)	*Synechococcus* sp.	Preetha *et al.* (2007)
Streptococcus sp.	Swain *et al.* (2009)	*Thalassobacter* sp.	Ninawe and Selvin (2009)
Streptomyces sp.	Das *et al.* (2010)	*Vibrio* spp.	Alavandi *et al.* (2004); El-Sersy *et al.* (2006); Thompson *et al.* (2010)
Vagococcus sp.	Sorroza *et al.* (2012)	*Zooshikella* sp.	Kim *et al.* (2010)
Weissella sp.	Cai *et al.* (1998)		

the most practical method for prawn probiotics (Huang *et al.* 2006). In contrast, the latter is the most commonly used in aquaculture (Austin *et al.* 1992; Gildberg *et al.* 1995, 1997; Gildberg and Mikkelsen 1998; Hai *et al.* 2009a) as most probiotics are designed to be mixed with feed (Gomes *et al.* 2009). Feed additives such as probiotics (*Lactobacillus rhamnosus*) improved the fecundity of zebrafish (*Danio rerio*) (Gioacchini *et al.* 2010). Oral administration provided advantages for prawns regardless of prawn size (Itami *et al.* 1998; Sakai 1999), such prawns can be treated at any stage of the culture period. Commonly, probiotics can be added directly into culture water (Gibson *et al.* 1998; Queiroz and Boyd 1998; Ringø and Vadstein 1998; Gram *et al.* 1999; Hai *et al.* 2009a) as water additives (Zhou *et al.* 2009; Cha *et al.* 2013), bathed in bacterial suspension (Hansen and Olafsen 1989; Smith and Davey 1993; Gram *et al.* 1999). The immersion method is also useful (Sung *et al.* 1994; Itami *et al.* 1998).

Single and combination

Probiotics can be applied singly or in combination (Havenaar *et al.* 1992; Gatesoupe 2002; Salinas *et al.* 2005; Kesarcodi-Watson *et al.* 2008, 2012a). Most studies on probiotics have focused on the use of single cultures, and it is largely speculative whether two or even multiple combinations of probiotic strains would be beneficial. Probiotics based on a single strain are less effective than those based on mixed strains (Verschuere *et al.* 2000; Hai *et al.* 2009a). Multistrain and multispecies probiotics enhanced protection against pathogenic infection (Timmermans *et al.* 2004; Kesarcodi-Watson *et al.* 2012a). A co-culture of *Roseobacter* BS 107 and *Vibrio anguillarum* enhanced the survival of larval scallop (Ruiz-Ponte *et al.* 1999). A mixture of *B. subtilis* and *Lactobacillus acidophilus* enhanced haemocrit values and serum bacteriocidal activity in Nile tilapia compared to those exposed to single cultures (Aly *et al.* 2008b). A mixture of *Pediococcus pentosaceus* and *Staphylococcus hemolyticus* decreased the prevalence of white spot syndrome virus (WSSV) in whiteleg prawns, *Litopenaeus vannamei* (Leyva-Madrigal *et al.* 2011). A mixture of *Lactococcus lactis* and *Lactobacillus plantarum* served as an immunostimulating feed additive, protected Japanese flounder against a challenge with *Streptococcus iniae* (Beck *et al.* 2015). In addition, positive effects of multistrain probiotics on the survival and growth of rohu (*Labeo rohita*) was seen at hatchling and fry stages, but not at later stages (Jha *et al.* 2015).

A combination of probiotics with prebiotics, immunostimulants or natural plant products has been used recently (Salminen *et al.* 1998; Hai and Fotedar 2009). A combined application of probiotics and prebiotics is called synbiotics, which is based on the principle of providing a probiont with a competitive advantage over competing endogenous populations, followed by improving the survival and implantation of the live microbial dietary supplement in the GI tract of the host (Gibson and Roberfroid 1995). Synbiotic feeding of *Enterococcus faecalis* and mannan oligosaccharide (MOS) showed better food conversion ratio (FCR) than either individual probiotic or prebiotic application alone (Rodriguez-Estrada *et al.* 2009). A combination of *Bacillus* spp. and MOS elevated the growth, survival and stress tolerance to low salinity in European lobster (*Homarus gammarus*) (Daniels *et al.* 2015). As applications of probiotics, prebiotics and synbiotics have elevated the survival of aquatic animals, the survival of animals was highest in the probiotic treatment, followed by the prebiotic and synbiotic ones (Decamp and Moriarty 2007; Daniels *et al.* 2015).

Enrichment

Enrichment of live feed with probiotics as encapsulations is an interesting idea, in which probiotics can remain viable or even proliferate on the live feed. Therefore, live feed can convey probiotics into the hosts effectively. Enrichment of live feed such as *Artemia* (Gatesoupe 1994; Hai *et al.* 2010b; Daniels *et al.* 2015), rotifer (Gatesoupe 1997), and copepods (Sun *et al.* 2013) with probiotics is considered as appropriate approaches. For instance, *Artemia* nauplii most effectively encapsulated a combination of *Pseudomonas synxantha* and *Ps. aeruginosa* for western king prawns, *Penaeus latisulcatus* (Hai *et al.* 2010b). Copepod (*Pseudodiaptomus annandalei*) is suitable to act as a vector of probiotics *Bacillus* spp. in grouper *Epinephelus coioides* larvae (Sun *et al.* 2013).

Live and dead/inactivated probiotics

A controversial issue is the effectiveness of live and dead probiotics in aquaculture. Live cells of *Kocuria* SM1 protected rainbow trout against challenge with *V. anguillarum* and *Vibrio ordalii* (Sharifuzzaman and Austin 2010b). Live probiotics were capable of producing cross-reactive antibodies against *V. harveyi* infections in rainbow trout, *Oncorhynchus mykiss* (Arijo *et al.* 2008). Diets with viable probiotics (live-spray and freeze-dried) induced a higher expression of the immune genes (TNF, TGF-β, IFN and Ig) than those with heat-killed probiotics (Panigrahi *et al.* 2011). Rainbow trout fed formalin killed or live *Enterobacter* C6-6 showed an increase in antibody against *Flavobacterium psychrophilum* (Lapatra *et al.* 2014). Cellular components and viable cells of *Bacillus licheniformis* and *Bacillus pumilus* increased the expression of lysozyme and respiratory burst of rohu (Ramesh *et al.* 2015). The phagocytic activity and complement activity of rainbow trout received *Lact. rhamnosus* JCM 1136 either live sprayed or freeze-dried were higher than those received heat-killed form (Panigrahi *et al.* 2005). A dietary supplementation with heat-inactivated probiotics stimulated the innate immune parameters of fish (Irianto and Austin 2003). Inactivated probiotic preparations appeared as an alternative to live probiotics, which could potentially cause safety problems in open aquatic environments (Salinas *et al.* 2006).

In contrast, the converse result is also true (Taoka *et al.* 2006b). Addition of formalized, sonicated, heat-killed and cell-free supernatant of probiotics conferred less protection in rainbow trout and Chinese drum (*Miichthys miiuy*) against pathogens, *Strep. iniae*, *Lactococcus garvieae*, *Aeromonas hydrophila* and *V. anguillarum* (Brunt and Austin 2005; Pan *et al.* 2008b). Nile tilapia fed dead-probiotics showed less resistance to *Edwardsiella tarda* infection than those fed live-probiotics (Taoka *et al.* 2006b). Live probiotics provide benefits to the host, while some either dead/inactivated cells or supernatant of probiotics also does the same, but other does not. Unfortunately, no evidence has proven that it is better to use live or dead probiotics. In addition, subcellular components of probiotics *Kocuria* SM1 and *Rhodococcus* SM2, and *Aeromonas sobria* GC2 and *B. subtilis* JB-1 protected rainbow trout against *V. anguillarum* (Sharifuzzaman *et al.*

2011) and *Yersinia ruckeri* (Abbass *et al.* 2010) respectively. Subcellular components and extracellular products are shown to be as effective as intact cells (Brunt and Austin 2005), but other work has contradicted these results (Taoka *et al.* 2006b).

Dosages

Overdosage administrations of probiotics can induce immune-suppression of continuous responses of nonspecific immune systems (Sakai 1999). A probiotic dosage may bring positive and negative results to different receivers, whose responses to different dietary probiotic levels have been observed (Panigrahi *et al.* 2004; Bagheri *et al.* 2008). A dietary supplement with *Lc. lactis* at 10^8 CFU g^{-1} improved the growth rate, lysozyme, antiprotease, serum peroxidase and blood respiratory burst activities of Japanese flounder (Heo *et al.* 2013). The application of *B. subtilis* and *B. licheniformis* in diets at 10^9 CFU g^{-1} improved FCR, specific growth rate, weight gain and protein efficiency ratio of rainbow trout fry (Bagheri *et al.* 2008). A diet supplemented with *Lactobacillus brevis* at 10^9 cells g^{-1} protected hybrid tilapia (*Oreochromis niloticus* × *Oreochromis aureus*) against *Aer. hydrophila* (Liu *et al.* 2013). Although rainbow trout fed a probiotic diet at either 10^9 or 10^{11} CFU g^{-1} showed higher head kidney leukocyte phagocytic activity, only the group that received the probiotic at 10^{11} CFU g^{-1} improved serum lysozyme and alternative complement activity compared to those without probiotics (Panigrahi *et al.* 2004). A multistrain mixture of probiotics at 10^7 CFU ml^{-1} was the best concentration of each probiotic for Greenshell™ mussel (*Perna canaliculus*) larvae (Kesarcodi-Watson *et al.* 2012a). Appropriate probiotic density is common at 10^5 CFU ml^{-1} (Guo *et al.* 2009; Hai *et al.* 2009a, 2010a; Zhou *et al.* 2009). Probiotics at 10^7 CFU ml^{-1} yielded stronger stimulatory effects due to an enhancement of cellular innate immune parameters (Salinas *et al.* 2006). A high dose did not result in a greater level of protection (Perez-Sanchez *et al.* 2013). Appropriate probiotic levels depend on the probiont species, fish species and their physiological status, rearing conditions and the specific goal of the applications (Merrifield *et al.* 2010b).

Time duration

The period of administration is also considered as an important factor in using probiotics. Studies have assessed potential probiotic applications for periods as short as 6 days (Jöborn *et al.* 1997), and more than 5 months (Aubin *et al.* 2005) or even 8 months (Aly *et al.* 2008c). Prolonged administrations of probiotics can induce immune-suppression of continuous responses of nonspecific immune systems (Sakai 1999). Notably, probiotics were unable to influence microbial community composition associated with cultured rotifers after feeding for 3 days (Qi *et al.* 2009). Supplementation of probiotics has proved to provide short-term benefits, but they were not detected within the GI tract for periods beyond 1–3 weeks (Robertson *et al.* 2000; Kim and Austin 2006; Balcázar *et al.* 2007a). While information on long-term efficacy is not available (Merrifield *et al.* 2010b), short-term supplementation has proven to be effective (Brunt and Austin 2005; Brunt *et al.* 2007; Newaj-Fyzul *et al.* 2007; Pieters *et al.* 2008). After 28 days of feeding with probiotics (*Shewanella xiamenensis* and *Aeromonas veronii*), the cumulative mortality of grass carp (*Ctenopharyngodon idellus*) challenged with *Aer. hydrophila* for 14 days, was reduced (Wu *et al.* 2015).

Constant supplementing of probiotics with diets may provide benefits (Merrifield *et al.* 2010b). Regarding long-term applications, Aubin *et al.* (2005) compared probiotic recovery levels over time, and observed that levels were higher after 20 days than after 5 months. Frequency of administration also plays a significant role in maintaining probiotic functions. During the culture period, a daily addition of probiotics is better than an every other day application (Guo *et al.* 2009). As probiotic colonization was transient in Atlantic cod larvae, continuous or repeated addition of probiotics to the fish larvae is needed (Skjermo *et al.* 2015). As with other immunostimulant products, short-term-cyclic probiotic feeding strategies may be beneficial to the hosts (Bricknell and Dalmo 2005), such strategies could involve a feeding regime of probiotic supplemented diets and unsupplemented diets alternately for short periods, cyclically. This application may provide direct benefits of short-term application during the supplemental feeding phase. During the unsupplemented stage, when gastric probiotic populations persisted for a number of weeks, probiotics provided protection against transient pathogens, and could continue to induce some degree of immunostimulation (Balcázar *et al.* 2007a).

Modes of actions

Colonization capacity

In terrestrial animals, one of the modes of actions of probiotics is a competitive exclusion, in which they enter digestive tracts, and then interfere with the action of potential pathogens by the production of inhibitory molecules and/or direct competition for space, nutrients or oxygen (Fuller 1989). In aquatic animals, there are two main modes of actions viz., competitive exclusion and immunomodulation. Probiotics occupy and colonize in digestive tracts, particularly the GI mucosal epithelium (Macey and Coyne 2006; Merrifield *et al.* 2010a; Lazado *et al.* 2011; Korkea-Aho *et al.* 2012) such as adherence (Mahdhi *et al.* 2012) and growth in intestinal mucus (Sorroza *et al.* 2012). Competition for adhesion receptors with pathogens may be the first probiotic effect (Montes and Pugh 1993). Thus they reduce the ability of pathogens (Chabrillon *et al.* 2005), and antagonize pathogens (Luis-Villasenor *et al.* 2011). Therefore, probiotics can be used as a suitable alternative to the prophylactic use of antibiotics and chemicals. They can compete for chemicals, nutrition/energy or even oxygen, enhance health and immune systems, elevate growth and survival rates as well as feed utility, and improve water quality. Although *Microbacterium* ID3-10, *Ruegeria* RA4-1, *Pseudoalteromonas* RA7-14 and *Vibrio* RD5-30 originated from Atlantic cod (*Gadus morhua*) larvae intestines, their colonization was just a transient presence in the larvae (Skjermo *et al.* 2015).

Antagonistic activity

Some bacterial species produce a wide range of antagonistic and antibiotic compounds that can be valuable as probiotics. Probiotics are used as an alternative to the prophylactic use of antibiotics (Decamp *et al.* 2008; Hai *et al.* 2009b; Heo *et al.* 2013) and chemicals (Decamp *et al.* 2008). They produced antibiotic compounds to compete for nutrients and sites (Moriarty 1998). Probiotics produced sufficient organic acid, along with an associated drop in pH, to antagonize many pathogenic bacteria (Ma *et al.* 2009). *Bacillus licheniformis* and *B. pumilus* showed antibacterial activity, tolerated low pH and high bile concentrations (Ramesh *et al.* 2015). *Lactobacillus* spp. produced various compounds viz., organic acids, diacetyl, hydro peroxide and bacteriocidal proteins (Rengpipat *et al.* 1998; Verschuere *et al.* 2000; Farzanfar 2006). These compounds activated the immune systems of animals, and rendered them more resistant to infections by viruses, bacteria, fungi and parasites (Raa 1996), or inhibited the bacterial pathogens in aquaculture systems (Rengpipat *et al.* 1998; Gram *et al.* 1999). *Bacillus licheniformis* CPQBA showed *in vitro* inhibitory characteristics against *Vibrio alginolyticus* in whiteleg prawns (Ferreira *et al.* 2015). Probiotics exhibited antagonism against pathogens (Guo *et al.* 2009) and antiviral effects (Wang *et al.* 2008).

Enhance immune responses

Probiotics increased in numbers of leucocytes (Merrifield *et al.* 2010a; Korkea-Aho *et al.* 2012), lymphocytes (Newaj-Fyzul *et al.* 2007; Aly *et al.* 2008a,c), monocytes (Aly *et al.* 2008c), erythrocytes (Abd El-Rhman *et al.* 2009; Sharifuzzaman and Austin 2010a,b), neutrophil adherence (Aly *et al.* 2008b), migration of neutrophils and plasma bactericidal activity (Taoka *et al.* 2006b), complement activity (Panigrahi *et al.* 2004; Sharifuzzaman and Austin 2010a,b; Sun *et al.* 2010), cytotoxicity (Salinas *et al.* 2005), phagocytic and superoxide dismutase activities (Sun *et al.* 2010; Zhou *et al.* 2010; Ridha and Azad 2012; Cha *et al.* 2013). An increase in total globulin (Sun *et al.* 2010; Korkea-Aho *et al.* 2012; Ridha and Azad 2012), albumin levels (Sharifuzzaman and Austin 2010a,b), serum bacterial agglutination titres (Ridha and Azad 2012), serum peroxidase and blood respiratory burst activities (Heo *et al.* 2013) have been presented. An enhancement of phagocytic, lysozyme (Sharifuzzaman and Austin 2010a,b; Sun *et al.* 2010; Ridha and Azad 2012), respiratory burst (Zhou *et al.* 2010; Korkea-Aho *et al.* 2011), antiprotease (Newaj-Fyzul *et al.* 2007) and peroxidase activities (Newaj-Fyzul *et al.* 2007; Sharifuzzaman and Austin 2010a,b) was discussed. *Bacillus pumilus*, and *B. licheniformis* and *B. pumilus* enhanced immune system of Nile tilapia (Aly *et al.* 2008c), and rohu (Ramesh *et al.* 2015) respectively.

Elevate health status and disease resistance

Probiotics conferred health benefits on Japanese flounder (Heo *et al.* 2013), black tiger prawns, *Penaeus monodon* (Rengpipat *et al.* 1998) and whiteleg prawns (Chiu *et al.* 2007), and western king prawns (Hai *et al.* 2010a). *Bacillus pumilus* enhanced health status, and disease resistance of Nile tilapia (Aly *et al.* 2008c). Probiotics promoted the defence of gut flora against pathogens (Skjermo and Vadstein 1999). As probiotics are an effective addition to disease control strategies in aquaculture (Irianto and Austin 2002a; Balcázar *et al.* 2006), a study conducted by Moriarty (1998) has reinforced this achievement in penaeid prawn ponds.

Probiotics have been shown resistance to diseases, and are excellent preventive tools against pathogens. Probiotics play an important role in creating resistance to infectious diseases, and in producing antibacterial materials that prevent pathogenic bacteria from getting into organisms. Numerous publications demonstrated the ability of probiotics in the protection of aquatic animals from pathogenic infection such as *Bacillus* spp. *vs Strep. iniae* (Cha *et al.* 2013), *Brevibacillus brevis vs Vibrio* spp. (Mahdhi *et al.* 2012), *Pseudomonas* M162 and M174 *vs Flavobacterium psychrophilum* (Korkea-Aho *et al.* 2012), *Vagococcus fluvialis vs Vibrio anguillarum* (Sorroza *et al.* 2012), *Phaeobacter* spp. *vs Vibrio anguillarum* (D'alvise *et al.* 2013), *Aeromonas media vs Vibrio tubiashii*

(Gibson *et al.* 1998), *Lactococcus lactis vs Strep. iniae* (Heo *et al.* 2013), *Lactobacillus* spp. *vs Aer. hydrophila* (Liu *et al.* 2013), *Bacillus mycoides vs Vibrio mimicus* (Ambas *et al.* 2013).

Probiotic *Pseudomonas* I-2 was used for the control of pathogenic vibrios (Chythanya *et al.* 2002). *Litopenaeus stylirostris* fed probiotic *Pedioccus acidilactici* showed resistance to vibriosis under pond conditions (Castex *et al.* 2008). Probiotic-fed whiteleg prawns showed effectiveness in reducing diseases caused by *Vibrio parahaemolyticus* (Balcázar *et al.* 2007c). Whiteleg prawns fed a mixture of *Ped. pentosaceus* and *Staph. hemolyticus* showed a decrease in the prevalence of WSSV (Leyva-Madrigal *et al.* 2011). *Bacillus licheniformis* and *B. pumilus* protected rohu against *Aer. hydrophila* infection (Ramesh *et al.* 2015). Consequently, probiotics protected aquatic animals from challenge with pathogens (Rengpipat *et al.* 1998).

Improve water quality

Probiotics have proven their effectiveness in improving water quality in different approaches. They enhanced decomposition of organic matter, reduced nitrogen and phosphorus concentrations, and controlled ammonia, nitrite, and hydrogen sulphide (Boyd and Massaut 1999; Ma *et al.* 2009; Cha *et al.* 2013). Probiotics reduced organic matter accumulation (Rengpipat *et al.* 1998; Verschuere *et al.* 2000), mitigated nitrogen (Wang *et al.* 2005) and phosphate pollution in the sediments (Wang and He 2009), and enhanced environmental conditions for a prawn farm (Suhendra *et al.* 1997). Probiotics reduced metabolic wastes during transportation of cardinal tetra (*Paracheirodon aexlrodi*) (Gomes *et al.* 2009). Probiotics improved water quality by reducing a number of pathogenic bacteria (Park *et al.* 2000; Dalmin *et al.* 2001).

Improve growth and survival rate

Applications of probiotics have improved aquatic animal growth rates, feed utility by influencing digestive enzyme processes, and survival rates. Bacterial strains promoted the growth of black tiger prawn nauplii (Maeda and Liao 1992), and giant freshwater prawn, *Macrobrachium rosenbergii* (Rahiman *et al.* 2010). *Pseudomonas aeruginosa* and *Ps. synxantha* improved the western king prawn growth (Hai *et al.* 2009b, 2010a). *Haliotis asinine* fed a diet pudding probiotic *Vibrio* Alg3.1Rf^R-Abn1.2Rf^R-enriched protein, exhibited a increased growth rate (Faturrahman *et al.* 2015). In fact, probiotics improved digestibility of feed (Deschrijver and Ollevier 2000; Ten Doeschate and Coyne 2008) due to enhancement of digestive enzymes (Zhou *et al.* 2009) viz., alginate lyases, amylases and proteases (Yu *et al.* 2009; Zokaeifar *et al.* 2012). Probiotics effectively participate in the digestive process by producing extracellular enzymes such as proteases, carbohydrolases and lipases, and by providing growth factors (Arllano and Olmos 2002; Ochoa and Olmos 2006). *Vibrio midae* SY9 enhanced digestive protease activity, protein digestion and absorption levels, and growth rate of *Haliotis midae* (Huddy and Coyne 2015). Photosynthetic bacteria and *Bacillus* spp. improved the growth of whiteleg prawns with an increase in lipase and cellulase activity (Wang 2007). The specific activities of amylase, total protease, and lipase were increased in the probiotic-fed *Fenneropenaeus indicus* (Ziaei-Nejad *et al.* 2006). In addition, an application of probiotics led to the generation of essential nutrients such as fatty acids (Vine *et al.* 2006), biotin and vitamin B12 (Sugita *et al.* 1991, 1992). Probiotics might act as a complementary food source or contribute to food digestion (Verschuere *et al.* 2000), as bacteria are one of the essential constituent food items in natural habitats by deposit-feeding holothurians (Moriarty 1978).

Vibrio C21-UMA and *V. midae* improved the survival of *Haliotis rufescens* (Silva-Aciares *et al.* 2011) and *H. midae* (Macey and Coyne 2006) respectively. The survival rate of Nile tilapia was increased when the fish was fed either *B. subtilis* or *Lact. acidophilus* (Aly *et al.* 2008b), and *Lact. acidophilus* (Villamil *et al.* 2014). *Pseudomonas aeruginosa* and *Ps. aeruginosa* YC58 improved the survival of pearl oyster (*P. mazatlanica*) juveniles (Aguilar-Macias *et al.* 2010), and the survival of Cortez oyster (*Crassostrea corteziensis*) larvae (Campa-Cordova *et al.* 2011) respectively.

Specific probiotic species

Several bacteria are harmful to one aquatic animal, but they can bring benefits to other species as probiotics. For instance, *Ps. aeruginosa* is well known as a member of the skin pathogenic microflora of both animal and human (Andonova and Urumova 2013), while they acted as a good probiotic for western king prawns (Hai *et al.* 2009a). In addition, *Ps. aeruginosa* in co-culture with *Burkholderia cepacia* promoted the growth and survival of lions-paw, *Nodipecten subnodosus*, (Granados-Amores *et al.* 2012). Dietary supplementation of *Ps. aeruginosa* improved innate immunity and disease resistance in rohu (Giri *et al.* 2012). *Streptococcus phocae* is known as a fish pathogen (Austin and Austin 2012), but they enhanced the growth of black tiger prawn post larvae and protected the animals against challenge with *V. harveyi* (Swain *et al.* 2009). *Aeromonas hydrophila* and *Aer. sobria* are proved as fish pathogens (Austin and Austin 2012), while they reduced infections of *Aeromonas salmonicida* (Irianto and Austin 2002b; a), *Lc. garvieae* and *Strep. iniae* (Brunt and Austin 2005) in rainbow trout. *Citrobacter freundii* has been associated with fish diseases (Austin and Austin 2012), but they are potential probiotics in Nile tilapia (Aly *et al.* 2008a,b). *Shewanella putrefaciens* is a fish pathogen (Austin and Austin 2012), but they were used as a probiotic in gilthead sea bream, *Sparus aurata*, and Senegalese sole, *Solea senegalensis* (De La Banda *et al.* 2012; Tapia-Paniagua *et al.* 2012).

Moreover, *Vibrio* is well known as a harmful bacteria genera for aquatic animals particularly for marine prawns, such as *V. harveyi*, *V. parahaemolyticus,* and *V. campbellii, V. vulnificus, V. anguillarum, V. alginolyticus, V. fluvialis* (Austin *et al.* 1995; Garriques and Arevalo 1995; Vandenberghe *et al.* 1999; Vijayan *et al.* 2006; D'alvise *et al.* 2013). In contrast, *V. alginolyticus* and *V. proteolyticus* are probiotics for Atlantic salmon (*Salmo salar*) (Austin *et al.* 1995) and turbot (*Scophthalmus maximus*) (Deschrijver and Ollevier 2000) respectively. *Vibrio fluvialis* is a probiotic for *Penaeus monodon* (Alavandi *et al.* 2004) and *Penaeus japonicus* (El-Sersy *et al.* 2006). *Vibrio* C21-UMA and *V. midae* improved the survival of abalone *H. rufescens* (Silva-Aciares *et al.* 2011) and *H. midae* (Macey and Coyne 2006) respectively. Therefore, the sub-strains or phylogenies need to be identified and considered carefully before use as specific probiotics for target fish species.

Suggestions for further directions

In the last decades, fish performance has improved considerably by the prophylactic use of probiotics as biological control agents. The optimal conditions for probiotics to survive, colonize, proliferate and provide their effects to the hosts properly in a particular environment needs to be considered, because the term 'one size fits all' cannot be applied to probiotics. There needs to be specific probiotic strains/species for target fish species in particular environments. Therefore, further work is needed to produce more detail to increase knowledge on particular probiotics for specific fish species.

As both Gram-positive and Gram-negative bacteria can be used as probiotics, it is of concern in the horizontal gene exchange to other animals including humans (Newaj-Fyzul *et al.* 2014). Resistance plasmids encoding for antibiotic resistance genes were transferred between pathogen and non-pathogenic Gram negative bacteria in sea water (Salyers 1995; Moriarty 1999). A consideration of the use of probiotics as antibiotics is needed as in many cases they are ineffective owing to an increase in virulence of pathogens. The issue of promoting the transfer of antibiotic resistance to human pathogens because of the use of probiotics needs further studies to provide evidence (Salyers 1995) and prevent this.

An in-depth research on probiotics should focus on other molecular methods to better understand the modes of action. Quorum sensing, different staining methods, transmission electron microscope, scanning electron microscope, polymerase chain reaction, fluorescent *in situ* hybridisation (FISH), gnotobiotic animals and high-through genomes technology could be used to create a better explanation of the present doubts in (i) adherence and colonization of probiotic and pathogenic bacteria, (ii) interactions between them within the digestive tracts, (iii) interaction between probiotics and host mucosa, (iv) gene expression and mucosal tolerance, (v) microvilli density and length, (vi) gene exchange or transfer. In manipulation of bacterial populations, the question is whether or not the domination of probiotics over other microbial populations by application of probiotics is correct, as they share the same living conditions. Quorum sensing is used to investigate the inhibition property of probiotics to other bacterial communities. To investigate the domination of potential probiotic ability, the FISH technique is used as a potential tool to characterize their dynamics and efficiency in the control of pathogenic bacteria (Del'duca *et al.* 2013). Lamari *et al.* (2013) proposed that the evaluation of probiotics should take into account ontogenetic chronology for improving larval quality.

Some studies have proved that the use of selected probiotics can be an alternative method for the protection of aquatic animals against diseases. However, farmers cannot predict when the onset of disease may occur to provide probiotic feeding in the weeks prior to infection. Therefore, further work on the effects of treatment is required if the onset has already occurred (Merrifield *et al.* 2010b). It is noted that a screen of promising probiotics plays a significant role in the selection of appropriate probiotics in aquaculture, as positive results *in vitro* sometimes fail to determine at *in vivo* effects (Kesarcodi-Watson *et al.* 2008). Moreover, the longevity of the health effect of probiotics is often uncertain. The fate of live probiotics in the aquatic environment is uncertain (Newaj-Fyzul *et al.* 2014). Although there are no data to support short-term-cyclic probiotic feeding strategies, it is assumed that this technique may avoid overstimulating the immune response whilst maintaining a level of protection or immunostimulation. Therefore, further research should investigate this application strategy properly (Merrifield *et al.* 2010b). Although synbioticum (Liu *et al.* 2010), and synbiotics (Rodriguez-Estrada *et al.* 2009) bring benefits to the hosts, they also need further investigation on kinds, proportions, time, and mixture methods.

Probiotic bacteria can improve the utilization of feed with a lower FCR by producing digestive enzymes, while the aquaculture sector is facing the problem of a shortage of fish meal for protein sources. Therefore, the role of probiotics in aquaculture becomes vital in collaboration with an alternative method to animal protein, by substituting plant protein sources. It is essential to investigate the metabolic capabilities of probiotics in the degradation of antinutrients to improve the nutritional value (Merrifield *et al.* 2010b), particularly in plant protein sources.

Dosage dependent studies are currently limited and somewhat contradictory. Further investigations are also needed before giving guidelines with any degree of confidence (Merrifield *et al.* 2010b). In addition, overdosages or prolonged administrations of probiotics induce immunosuppression of continuous responses of the hosts (Sakai 1999). Although there are not many evidences about prolonged administration of probiotics in aquaculture, the Sakai (1999)'s hypothesis that on converse results or even death, if probiotics are applied at overdosages, over a long period of time, and indiscriminate frequency, need further studies. These investigations can also help to maintain an efficient immune system, which is reflected in fish quality and productivity.

All in all, further in depth, investigations on every single aspect of probiotics will bring desired results in the use of probiotics in aquaculture, when the mechanisms of probiotics in aquaculture are not far from being completely understood. Therefore, probiotics, applicable in large-scale aquaculture, will have to be produced and formulated under industrial conditions that conform to quality control guidelines. Consequently, these further works will globally provide organic aquatic products, which are necessary for the safe human consumption of food and health security.

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Conflict of Interest

There is no conflict of interest.

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