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REVIEW

Update on the use of yeast in shrimp aquaculture: a minireview

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Abstract Growth in shrimp farming has shown an expansion of rearing farms and intensification of production methods, which have affected shrimp health, growth and survival and environmental integrity of the coastal areas, making the long-term viability of this farming industry doubtful. This industry demands alternative strategies to improve shrimp production, enhance disease resistance and take good care of the environment. Yeasts (live cell, total cell, or their active by-products) confer a benefit to the host by providing nutrition and protection against pathogens. This review summarizes the current knowledge of yeast species on: (i) shrimp aquaculture; (ii) shrimp nutrition; (iii) shrimp immunity; (iv) water and environment. Yeasts are used as alternative feed ingredients in aquaculture because of their nutritional value. Some products, such as β-glucans, chitin, nucleic acids, mannan oligosaccharides, β-carotene, B-complex, torulene, and torularhodin have been used in shrimp diets, showing direct effect on shrimp growth. Amylases, chitinases, phytases, and proteases are used to enhance gut maturity and digestive enzyme activity in shrimp larvae. The immune and antioxidant proprieties of yeasts have an important role as probiotics and immunostimulants to enhance shrimp resistance against common viral and bacterial diseases. Yeast bioactive products, such as glucans, nucleotides, polysaccharides, carotenoid pigments, lipids, proteins, and vitamins, activate the immune response directly or improve intestinal microbiota, specially glucans, which enhance shrimp circulating hemocytes (THC), phagocytosis, encapsulation, ProPO activity and melanization. Different yeast species, such as *Debaryomyces* sp., *Candida* sp., *Rhodosporidium* sp., *Saccharomyces* sp., and *Yarrowia* sp. have recently gained popularity as beneficial candidates in farmed organisms to maintain health conditions and well-being of different aquatic animals, including rearing shrimp. In addition, this study condensed current knowledge of the ability of yeasts to sustain the performance of marine shrimp and provide information for future research and development of yeast application in aquaculture.

Keywords Aquaculture . Environment . Growth . Health . Shrimp . Yeast

Introduction

Fish and shellfish are important protein sources for global human food consumption (Pahlow et al. 2015),

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and aquaculture has helped to meet this demand to such an extent that it is currently considered as the fastest growing animal food production for human beings (Ottinger et al. 2016). Among shellfish, shrimp are the most important commercial crustacean aquaculture species worldwide and especially in Southeast Asia and China. Nevertheless, the industry has been consistently affected with a great production loss from the outbreak of infectious diseases, particularly from viruses and bacteria (Flegel 2007).

Rapid and uncontrolled growth of pathogens in aquatic organisms and the excessive use of antibiotics to prevent them have resulted in the emergence of several resistant pathogens as some viruses, such as Taura syndrome virus (TSV), white spot syndrome virus (WSSV), yellow head virus (YHV), and gill-associated virus (GAV) (Lightner 2011) besides *Vibrio* species as *V. campbelli*, *V. fluvialis*, *V. harveyi*, *V. parahaemolyticus*, *V. vulnificus* (Kang et al. 2014; Yano et al. 2014). Particularly, acute hepatopancreatic necrosis disease (AHPND) is caused by *V. parahaemolyticus*, which has resulted in massive mortalities in shrimp farms (Joshi et al. 2014; Junprung et al. 2019). The previously mentioned pathogens are impeding development and sustainability of the industry worldwide (Bondad-Reantaso et al. 2005). The demand for an increase in food quality continues, and the side effects of antibiotics have become an increasing threat to humans; the use of antibiotics should be eliminated, reduced or replaced with new products, those that could enhance environmental protection (Arias-Andres et al. 2014; Siriyappagouder et al. 2014). Alternative methods of disease prevention have been designed via antioxidant systems, bioremediation, genetics, immunostimulants, nutrition, probiotics, prebiotics, symbiotics, and so on (Faggio et al. 2015).

Yeasts are unicellular basidiomycetes and ascomycetes with budding or fission reproduction. Most likely only 1% of the total yeast species is known (Fell 2001), and those microorganisms have shown the potential to produce many bioactive substances, such as glucans, glutathione, toxins, enzymes, phytase and vitamins with application in aquaculture, chemical, cosmetics, food, environmental protection, and pharmaceutic industries (Sarkar and Bhaskara 2016).

Yeasts are a popular product to use in aquaculture (whole or fractions) as supplements in animal feed as source of amino acids, proteins, and vitamins, principally B-complex with positive effect on shrimp growth and immunity (Chotikachinda et al. 2008; Ferreira et al. 2010; Gamboa-Delgado et al. 2016; Álvarez-Sánchez et al. 2018). Yeasts are used on bioremediation of water quality to clean up contaminated soil and reduce nitrogen from metabolism excretion (Deng et al. 2013; Jin et al. 2018). Other yeast use in aquaculture is for disease (bacteria or virus) control and application reduction of antibiotics and other chemical products that affect microorganism resistance or pathogenesis (Balcazar et al. 2006; Biswas et al. 2012; Babu et al. 2013).

Another important feature of yeast is that it is resistant to antibiotics (Blackburn and Avery 2003). Some prokaryotic bacteria used as probiotics have the ability to transfer plasmid with antibiotic resistant genes to pathogens in the gastrointestinal tract of the host (Verraes et al. 2013). However, this phenomenon has not been detected in probiotic yeast (Kourelis et al. 2010). This review summarizes the current knowledge of the main yeast strains used as probiotics, feed additives or immunostimulants to reduce feed costs, enhance growth and survival in shrimp culture. The information provided is focused on works that directly used yeast and its products, showing their effects on metabolism, digestion, physiology, immune system, water quality and bioremediation.

Yeast application in aquaculture industry

Aquatic animals interact with a high and diverse range of microorganisms, which could play a vital role on their environmental condition, growth, and survival. The management of aquaculture conditions leads to the creation of negative or favorable environments to microorganisms with their respective effect on those aquatic animals (Aguirre-Guzman et al. 2009). Yeasts are microorganism species normally found in natural shrimp farming environments where their role in health and nutrition has been documented. These microorganisms have been used alive to feed live organisms or after processing them as feed ingredients. Yeast species as *Candida* sp., *C. utilis*, *C. sake*, *C. tropicalis*, *Debaryomyces* sp., *D. hansenii*, *Hanseniaspora* sp., *Kloeckera* sp., *Kluyveromyces* sp., *Leucosporidium* sp., *Metschnikowia* sp., *Pichia* sp., *Rhodotorula* sp., *R. rubra*, *R. glutinis*, *Saccharomyces* sp., *S. cerevisiae*, *Sporobolomyces* sp., *Trichosporon* sp. and *Yarrowia* sp. have shown application in shrimp aquaculture of *Litopenaeus vannamei*, *Penaeus monodon*, *Marsupenaeus japonicus*, *F. indicus*, etc. (Burgents et al. 2004; Sajeevan et al. 2006; Zhenming et al. 2006;

Table 1 Effect of yeast on growth parameter of shrimp species with aquaculture interest

Yeast	Shrimp	Doses	Use	References
Candida. sake, C. utilis, Debaryomyces hansenii	*Fenneropenaeus indicus postlarvae*	20%	Diet supplementation (weight gain)	Sarlin and Philip (2016)
C. utilis	*L. vannamei*	60%	Diet supplementation (fish meal replacement)	Gamboa-Delgado et al. (2016)
Rhodosporidium paludigenum	*L. vannamei*	1% (10^8 yeast g^{-1} diet)	Probiotic (weight gain, specific growth rate, survival, and feed conversion ratio)	Yang et al. (2010)
Saccharomyces cerevisiae	*Fenneropenaeus indicus*	50%	Diet supplementation (fish meal replacement)	Sharawy et al. (2016)
S. cerevisiae (baker's yeast extract)	*L. vannamei*	1%	Diet supplementation (weight gain, specific growth rate, and feed conversion ratio),	Jin et al. (2018)
S. cerevisiae (Baker's yeast)	*P. monodon*	0.7-1.3%	β-glucan diet supplementation (growth, specific growth rate) and survival)	Felix et al. (2008)
S. cerevisiae	*P. monodon*	1-2 g kg^{-1}	Dietary supplementation of mannan oligosaccharide (Growth, THC, epithelium layer and cell density of the gut).	Sang et al. (2014)
S. cerevisiae (Bio-Mos)	*L. vannamei*	2-8 g kg^{-1}	Dietary supplementation of mannan oligosaccharide (Weight gain, specific growth rate, intestinal microvilli length, SOD)	Zhang et al. (2012)
S. cerevisiae (DV Aqua)	*L. vannamei*	1-1.5 g kg^{-1}	Growth	Deng et al. (2013)
S. cerevisiae (flash dried yeast)	*L. vannamei*	30%	Shrimp digestion	Qiu et al. (2018)
S. cerevisiae (Aqua-Myces)	*L. varmamei*	0.2 -4 g kg^{-1}	Dietary application of mannan oligosaccharide (growth and survival composition)	Genc and Ebeoglu (2013)
S. cerevisiae (Aqua-Myces)	*P. semisulcatus*	3 g kg^{-1}	Dietary application of mannan oligosaccharide (growth, body composition and hepatopancreas histology)	Genc et al. (2007)

Biswas et al. 2012; Babu et al. 2013; Zhao et al. 2017; Álvarez-Sánchez et al. 2018; Xiong et al. 2018). A better understanding of their use and modes of action help to know about the appropriate applications in aquatic systems. Tables 1-2 show recent yeast applications on shrimp farming.

Effect on shrimp growth

Effect as feed additive

Traditional ingredients used for shrimp aquaculture (fishmeal and oil) have declined their production in recent years. Several alternative ingredients have been tested to replace fishmeal in aquaculture diets, including vegetable and microbial sources. Yeasts from industrial process are by-products used as emerging alternative feed ingredients in aquaculture because of their nutritional value (proteins, lipids, vitamins, minerals, etc.) and some bioactive compounds, such as β-glucans, chitin and nucleic acids (Sarlin and Philip 2011; Babu et al. 2013; Øverland and Skrede; 2016; Zhao et al. 2017). Different types of yeasts (*C. utilis*, *D. hansenii*, *R. paludigenum*, *S. cerevisiae*) and their extracts have been used in aquaculture diets for shrimp (*F. indicus, L. vannamei*, and *P. monodon*) at different levels (1-60% or 0.2-8 g kg^{-1}) (Table 1), as fishmeal replacement or additive feed (Gamboa-Delgado et al. 2016; Sharawy et al. 2016; Jin et al. 2018). Sarlin and Philip (2016) used different species and yeast strains as supplements in shrimp post-larvae (*F.*

indicus). Those yeasts displayed protein, lipid, and carbohydrate contents from 22.00 to 30.00, 2.00 to 8.25 and 22.36 to 29.68%, respectively, without any difference in their biochemical composition. This study demonstrated that *C. sake*, *C. utilis* and *D. hansenii* supported better growth and survival in shrimp compared to other strains, confirming that marine yeasts may serve as potential feed supplements in shrimp. Gamboa-Delgado et al. (2016) found similar results in the use of *C. utilis* on *L. vannamei* where 60% of yeast incorporation in shrimp diet showed a similar dietary contribution than fishmeal. Other yeast species that have been used on shrimp with dietary purpose are *R. paludigenum* and *S. cerevisiae* (Table 1).

Some studies reported yeast strains as immunostimulants included in shrimp diet. Deng et al. (2013) evaluated commercial *S. cerevisiae* at different doses (1.0 and 1.5 g/kg shrimp diet) where *L. vannamei* fed with yeast as diet supplement displayed better final body length, feed conversion rate and survival ($P < 0.05$) of shrimp juveniles. Similar effect was found by Jin et al. (2018) where dietary effect of 1% of *S. cerevisiae* in shrimp diet showed a significant ($P < 0.05$) enhancement of growth parameters. However, an excess of this yeast on shrimp diet could also have negative effects on final body weight, survival, specific growth rate and weight gain (Sharawy et al. 2016). The authors reported that 50% substitution of fermented soybean meal by *S. cerevisiae* was according to *F. indicus* post-larvae rearing. Some products, such as β-glucan and mannan oligosaccharide (1-8 g/kg shrimp diet) from *S. cerevisiae* have been used in shrimp diet (*L. vannamei*, *P. monodon*, *P. semisulcatus*) with significant results on weight gain, specific growth rate or survival (Genc et al. 2007; Felix et al. 2008; Zhang et al. 2012; Genc and Ebeoglu 2013; Sang et al. 2014). Those products have been used as protein and amino acid source showing efficient effect on the use of dietary protein with a direct effect on shrimp growth.

Marine red yeasts are normal microbiota in shrimp farming and wild shrimp environments. Some yeast species are abundant in carotenoid product (β-carotene, torulene, and torularhodin) as *Rhodosporidium paludigenum* (Yang et al. 2010, 2011). Dietary supplementation (1 g/100 g) of dry or live *R. paludigenum* (10^8 yeast cells g^{-1} shrimp diet) significantly increased *L. vannamei* survival, specific growth rate and weight gain (Yang et al. 2010).

Digestive system, microbiota, gut structure and ontogeny

The shrimp digestive system consists of mouth, foregut, midgut, hindgut, and hepatopancreas. The mouth is located on the ventral surface of the head region where feed is introduced after mastication by the maxilliped. The foregut, including the esophagus and stomach, is a specialized part with grinding activity. The stomach has a connection with the hepatopancreas, which is the primary organ of nutrient digestion, absorption, and storage (Aguirre-Guzman and Ascencio-Valle 2000). In addition, this organ is a major part of the posterior cephalothorax. The stomach and hepatopancreas have connections with the midgut that show a high absorption surface. The hindgut or intestine is a tube that runs from the cephalothorax to the rectum and anal canal, which transports feed waste and generates fecal products. All the digestive system is covered with epithelium cells where microorganisms establish and execute their functions (Aguirre-Guzman and Ascencio-Valle 2000).

Intestinal microbiota is a complex ecosystem with an important role in host nutrition, which change during the host's life stage (adult, juvenile or post-larva), physiology condition (diseases, growth, reproduction, stress, hormone secretion) environment (culture, laboratory, wild), water quality (oxygen, pH, temperature, salinity, etc.) and feed sources (Tuyub et al. 2014; Li et al. 2018). The relationship between intestinal microbiota and shrimp, their composition, changes, and gut environment are important factors to understand the ecological succession mechanisms of gut microbiota and their effect on shrimp nutrient acquisition. However, the study of shrimp gut microbiota has become a focus to understand the microorganism composition and function by methodological comparisons. Conventional microbial methods have been used, such as denaturing gradient gel electrophoresis and 16S rRNA studies where microbial isolates are a small proportion of all the microorganisms associated to animal, gut, and environment, and do not represent the real diversity and quantity of the shrimp intestine (Li et al. 2018).

Microbiota is an important element to shrimp life with metabolic, trophic and protective functions (Tuyub et al. 2014). Yeasts are part of normal microflora of organisms and sediments of shrimp culture areas where different genus have been isolated, such as: *Brettanomyces* sp., *Bullera* sp., *Candida* sp., *Clavispora* sp., *Cryptococcus* sp., *Debaryomyces* sp., *Deidium* sp., *Dekkera* sp., *Dipodascus* sp., *Filobasidium* sp., *Galactomyces* sp., *Geotrichum* sp., *Guehomyces* sp., *Hanseniaspora* sp., *Hansenula* sp., *Issatchenkia* sp., *Kazachstania* sp., *Kluyveromyces* sp., *Kodamaea* sp., *Leucosporidium* sp., *Lodderomyces* sp., *Metschnikowia* sp., *Mrakia* sp., *Phaeotheca* sp., *Pichia* sp., *Pseudozyma* sp., *Rhodotorula* sp., *Rhodosporidium* sp., *Saccharomyces* sp., *Sporobolomyces* sp., *Torulopsis* sp., *Trichosporon* sp., *Williopsis* sp., *Wingea* sp., *Yarrowia* sp., *Zygowilliopsis* sp. and *Zygoascus* sp. (Sajeevan et al. 2009a,b; Sukumaran et al. 2010; Yang et al. 2010, 2013; Babu et al. 2013; Navarrete and Tovar-Ramírez 2014; Wilson et al. 2015; Sarkar and Bhaskara-Rao 2016). Those yeasts (total cell, live, or their metabolic products) are poorly known and show high potential applications in shrimp farming.

Ontogeny of the shrimp digestive system has been the subject of studies in the last year reporting the use of yeast to enhance gut maturation and digestive enzyme activity (Álvarez-Sánchez et al. 2018). The development of gastrointestinal tract microbiota is a gradual process along shrimp life where their colonization in the gastrointestinal tract occurs when the anal pore shows drinking movement (fifth nauplii stage), and the mouth opens to the exterior environment (Li et al. 2018). Zhang et al. (2012) reported a higher contact surface and nutrient absorption in the intestine of several crustacean species by including mannan oligosaccharides (MOS) in the diet. Xiong et al. (2018) found similar results where a higher microvillus height occurred in *L. vannamei* fed 50 g/kg yeast nucleotide. However, Genc et al. (2007) and Genc and Ebeoglu (2013) investigated the effects of MOS from yeast (*S. cerevisiae* outer cell wall) on hepatopancreas histology of *P. semisulcatus* post-larvae (Pl 20) and *L. vannamei* juvenile, respectively. They found an effect on histomorphology of the microtubular structure of hepatopancreas tissues and R cell, which were used to evaluate the nutritional condition of shrimp and enzyme activity.

Effect on digestive enzymes

Shrimp have shown digestive enzymes as proteases (trypsin, pepsin, *carboxypeptidase* A, B, *leucine aminopeptidase, arylamidase), lipases, esterases, and* carbohydrases (amylases, maltase, chitinase and cellulase) which are directly associated with feed digestion and nutrient absorption (Jing et al. 2009; Zhao et al. 2017; Qiu et al. 2018). The use of yeast with dietary purpose might have stimulated enzyme production in shrimp, contributing to development, digestion, nutrition, and health. In addition, some yeasts are available to produce extracellular enzymes (amylase, chitinase, phytase, protease, etc.) and bioactive substances (astaxanthin, β-carotenoid, glutathione, polyamine, trehalose, killer toxin, etc.) with potential relevance in digestive processes and nutrient absorption that provide energy to organisms (Zhenming et al. 2006; Jing et al. 2009; Zhao et al. 2017).

Jing et al. (2009) isolated yeast strains from seawater, sediments, and organisms finding that *Aureobasidium pullulans*, *Y. lipolytica, I. orientalis* and *Cr. aureus* were capable of producing an extracellular alkaline protease. Bessadok et al. (2015) found that *Y. lipolytica* strain from shrimp by-products showed proteolytic activity. Amylase, cellulases, chitinase, lipases, phytase, protease were detected in marine yeast (*A. pullulans, C. rugosa, C. intermedia, C. parapsilosis, C. quercitrusa, C. kefyr, Cr. aureus, D. cantarelli, Ko. ohmeri, K. marxianus, K. fragilis, L. elongisporus, Me. reukaufii, P. guilliermondii, R. mucilaginosa, Y. lipolytica, Sporotrichum* sp.) with potential use in aquaculture activates and biotechnology (Navarrete and Tovar-Ramírez 2014; Zhenming et al. 2006; Sarkar and Bhaskara 2016; Álvarez-Sánchez et al. 2018). Ferreira et al. (2010) demonstrated that *Saccharomyces* yeast cells contained vacuolar proteases of serine, aspartyl, metallo-proteases, and pectinases; Table 1 displays the use of *S. cerevisiae* on *Fenneropenaeus indicus*, *L. vannamei*, *P. semisulcatus, P. monodon* with dietary purpose and where enzymatic effect on digestion, growth and other physiology process have been suggested.

Yeasts can grow rapidly in the intestine and produce extracellular proteases, which represent a small part to total enzyme activity of the shrimp gut (Nimrat et al. 2017). The enzymes produced help increasing the digestive utilization of feed or detoxifying injurious metabolites released by other microorganisms. In addition, those microorganisms stimulated enzyme production in shrimp hepatopancreas. Zhao et al. (2017) reported a significant increase of trypsin activity in *L. vannamei* hepatopancreas with the use of dietary yeast extract. However, they also reported a decrease of lipase activity. Zhang et al. (2012) reported a higher contact surface and nutrient absorption in the intestine of several crustacean species by including mannan oligosaccharides (MOS) in the diet (Table 1). Gut microvilli are associated to shrimp digestion and help to generate a better condition for shrimp growth and health. Xiong et al. (2018) reported higher microvillus height in *L. vannamei* fed with 50 g/kg yeast nucleotides in diet.

Yeast effect on shrimp immunity and infection

Yeasts have an important role to enhance shrimp resistance against common diseases. Their use with antioxidants, immunology (natural or non-specific immunity), nutritional, probiotics, stress-less purposes in shrimp has improved their health. Different studies have shown the use of yeast (total cell, live, or their bioactive products) in shrimp immunology components. Those products have been used in shrimp health as anticoagulant proteins, agglutinins, antimicrobial peptides or AMPs (defensins and chemokines), antiapoptotic protein encapsulation, and bacteriocins. They have also been used as free radicals, formation of nodules and humoral components, lysozymes, monostatin, phagocytosis, phenol oxidase enzyme, proteases, hydrogen peroxide, siderophores, gramicidin, polymyxin, and tyrotricidin (Burgents et al. 2004; Zhenming et al. 2006: Sajeevan et al. 2009a,b; Bai et al. 2010, 2014; Babu et al. 2013; Deng et al. 2013; Sang et al. 2014; Wilson et al. 2015; Neto and Nunes 2015; Jin et al. 2018). The use of yeasts as a shrimp health tool is one of the most frequent in aquaculture, whose applications are indicated below.

Disease prevention

Diseases caused by bacteria or viruses affect the organisms under rearing and generate serious economic losses to the shrimp industry. An alternative strategy for disease control is the use of yeasts, their products or fractions to improve shrimp health and generate resistance to pathogens. The use of antibiotics and chemotherapeutants are undesirable in shrimp farms as disease control. In addition, vaccines are not effective against many bacterial diseases (Felix et al. 2008). Yeasts have excellent nutritional content and functional properties, including a role as probiotics and immune stimulants. Some products, as β-glucan and nucleotides derived from yeasts (*K. fragilis* and *S. cerevisiae*) have been used on *L. vannamei* and *P. monodon* stimulation, providing resistance to vibriosis generated by *V. alginolyticus* and *V. parahaemolyticus* (Felix et al. 2008; Guo et al. 2016). Moreover, β-glucans from yeast (Table 2) were used as protective agents against infectious myonecrosis virus (IMNV) and WSSV in *L. vannamei, M. japonicus, and P. monodon* (Sukumaran et al. 2010; Zhu and Zhang 2012; Neto and Nunes 2015; Wilson et al. 2015). Those results have demonstrated the immunostimulatory activity of yeast glucans against shrimp viruses, which detected the activation of genes of different immune factors, antimicrobial peptide, anti-lipopolysaccharide factor, penaeidin, prophenoloxidase (ProPO), and superoxide dismutase (SOD). The use of glucans and other yeast products as immunostimulants is an interesting prophylactic strategy to control infections and decrease the use of chemotherapeutic products in shrimp farming with corresponding environmental advantage.

Effect on immunological parameters

Immunostimulants are products that can promote and induce a strong defense response in the host (Aguirre-Guzman et al. 2009; Ringø et al. 2012). The yeast products with this activity include bioactive products, carotenoid pigments, glucans, lipids, nucleotides, polysaccharides, proteins, and vitamins (Aguirre-Guzman et al. 2009; Babu et al. 2013; Sang et al. 2014; Mohan et al. 2019), which activate the innate immune system directly or improve growth of intestinal microbiota. Based on previous reports in crustaceans, immunostimulants can increase phagocytosis of pathogens by activating phagocytic cells in the hemolymph, increasing antibacterial and antiseptic properties of hemolymph, activating the ProPO system and mediating signal recognition and phagocytosis (Bondad-Reantaso et al. 2005; Castex et al. 2010).

Table 2 shows the yeast species used with immunostimulatory purpose in shrimp species. Shrimps fed 10% yeast diet at a feeding frequency of once every week showed significantly higher immune response compared to the control. *C. aquaetextoris* showed a potential immunostimulation in *P. monodon* when it was incorporated in diet aids and used as prevention and/or treatment of diseases in tiger shrimp. Better immunostimulatory property of *C. aquaetextoris* whole-cell yeast diet fed group could be attributed to the

Table 2 Effect of yeast against pathogens of shrimp species with aquaculture interest

Yeast	Shrimp	Doses	Use	References
C. aquaetextoris	*Penaeus monodon*	10%	Protection against WSSV infection and genes expression of hematological and immune peptides and proteins.	Babu et al. (2013)
C. haemulonii, C. oceani, C. parapsilosis, C. spencermartinsiae, D. fabryi, D. nepalensis, Hortaea werneckii, Meyerozyma guilliermondii	*P. monodon*	0.2%	Immunostimulants with β-glucan and resistance to WSSV infection	Wilson et al. (2015)
C. sake	*F. indicus*	10%	THC, PO, NBT immunostimulation and survival to WSSV infection	Sajeevan et al. (2006)
C. sake	*F. indicus*	0.2%	β-glucan immunostimulation and survival to WSSV infection	Sajeevan et al. (2009a)
C. sake	*F. indicus*	0.2%	Immunostimulation and survival to WSSV infection	Sajeevan et al. (2009b)
C. tropicalis, D. hansenii	*P. monodon*	0.2%	β-glucan diet supplementation (resistance to infectious WSSV)	Sukumaran et al. (2010)
C. sake, C. utilis, D. hansenii	*F. indicus*	20%	Resistance to WSSV infection	Sarlin and Philip (2016)
Rhodotorula minuta	*P. monodon*	10%	Source of immuno-stimulant	Subramanian et al. (2014)
R. paludigenum	*L. vannamei*	1% (10^8 yeast g^{-1} diet)	Antioxidant competence, activity of catalase, SOD, glutathione peroxidase in serum and hepatopancreases,	Yang et al. (2010)
R. paludigenum	*L. vannamei*	1%	Stimulation of antioxidant genes in hepatopancreas	Yang et al. (2013)
S. cerevisiae (Baker's yeast extract)	*M. japonicus*	0.1 mL (36.7% yeast nucleotides)	Immunostimulants (expression of anti-microbial peptides/proteins) and resistance to *V. nigripulchritudo*)	Biswas et al. (2012)
S. cerevisiae	*L. vannamei*	2 g/kg diet (0.2%)	Immunostimulation with β-glucan (THC, ProPO, SOD)	Bai et al. (2010)
S. cerevisiae	*L. vannamei*	0.1%	Immunostimulants with β-glucan (THC, ProPO, respiratory burst, SOD) and resistance to WSSV infection	Bai et al. (2014)
S. cerevisiae	*L. vannamei*	1 g kg^{-1}	β-glucan diet supplementation (resistance to IMNV)	Neto and Nunes (2015)
S. cerevisiae	*L. vannamei*	1%	Resistance to *Vibrio campbellii* infection	Burgents et al. (2004)
S. cerevisiae	*M. japonicus*	20 µg/g	Injected β-glucan-encapsulated (resistance to infectious WSSV)	Zhu and Zhang (2012)
S. cerevisiae (Baker's yeast extract)	*L. vannamei*	1%	Immunostimulants (expression levels of the immune-related genes of intestine and hepatopancreas), and resistance of ammonia nitrogen stress	Jin et al. (2018)

Table 2 Continued

Yeast	Shrimp	Doses	Use	References
S. cerevisiae (Baker's yeast)	*P. monodon*	0.2%	Immunostimulation of hemocytes with β-glucan, and ProPO activation	Thanardkit et al. (2002)
S. cerevisiae (Baker's yeast)	*P. monodon*	0.7-1.3%	β-glucan diet supplementation resistance to *Vibrio alginolyticus*	Felix et al. (2008)
S. cerevisiae (Bio-Mos)	*P. monodon*	1-2 g kg^{-1}	Dietary supplementation of mannan oligosaccharide (Growth, THC, epithelium layer and cell density of the gut).	Sang et al. (2014)
S. cerevisiae (Bio-Mos)	*L. vannamei*	2-8 g kg^{-1}	Dietary supplementation of mannan oligosaccharide (SOD and resistance against NH_3 stress)	Zhang et al. (2012)
S. cerevisiae (DV Aqua)	*L. vannamei*	1-1.5 g kg^{-1}	Reduced endotoxin in shrimp intestine, activation of lysozyme and PO, and stimulate total hemocytes level.	Deng et al. (2013)
S. uvarum (Spent brewer's yeast slurry)	*P. monodon*	0.2%	Immunostimulants with β-glucan (ProPO)	Suphantharika et al. (2003)
Kluyveromyces fragilis (Rovimax Nx)	*L. vannamei*	60-120 mg kg^{-1}	Immunostimulation with nucleotide (SOD, total nitric oxide synthase and lysozyme)	Guo et al. (2016)
S. cerevisiae	*L. vannamei*	1-2 g kg^{-1}	Better level of THC and granular hemocyte count	Chotikachinda et al. (2008)
S. cerevisae + FOS	*L. vannamei*	50-400 mg kg^{-1}	Increase of THC level of THC	Rivera et al. (2019)

cellular constituents of yeasts including mannan, chitin, glucan, nucleotides, carotenoid pigments, lipids, proteins and vitamins (Babu et al. 2013) (Table 2). The use of MOS in crustacean aquaculture has been studied in many countries. It is a complex of carbohydrates that has been isolated from the cell wall of the yeast *S. cerevisiae,* which prevent the adhesion of bacterial pathogens because they act by blocking adherence of microbial lectins with the carbohydrates present on the surface of the intestinal cells. The prevention of adhesion inhibits colonization of infective pathogen process (Genc et al. 2007; Zhang et al. 2012; Genc and Ebeoglu 2013; Sang et al. 2014).

Immunological cells

Hemocytes (hyalinocytes, granulocytes and semi-granulocytes) are important components present in hemolymph that participate in clotting, encapsulation, nodule formation, phagocytosis, proPO activation, tissue repair. In addition, they help in production of adhesion molecules, agglutinins, and AMPs. Hemocytes also have inhibitory enzymes needed for regulating the proteolytic cascade, preventing its over stimulation and the resultant tissue damage while also producing cytotoxic molecules, such as lysozyme, phosphatase, esterase, phospholipase, peroxidase, protease, etc. (Aguirre-Guzman et al. 2009). The total hemocyte count (THC) is a parameter used for immune condition on shrimp, whose cells have been stimulated by yeast products (total cell, live, or their metabolic products). Deng et al. (2013) and Bai et al. (2014) found a decrease of THC on *L. vannamei* during a bioassay when *S. cerevisiae* increased in shrimp, which represented an immunostimulation of hemocytes with *posteriori* decrease in total number. Similar results were detected by Sajeevan et al. (2009a) when using β-glucan from *C. sake* on the immunity of *F. indicus* detecting a significant decrease on THC after immnostimulation. However, Sajeevan et al. (2006) showed that *F. indicus* fed a diet with *C. sake* (10%, w/w) exhibited a significantly higher level of THC pre- and post-infection with WSSV compared to the control treatment and suggested an immunostimulatory effect of the yeast on shrimp. Rivera et al. (2019) demonstrated a high THC in *L. vannamei* fed with a mixture of fructoligosaccharides (FOS) and *S. cerevisiae* (50, 100, 200 and 400 mg yeast + FOS /kg of commercial diet) compared to the control treatment (Table 2). Sang et al. (2014) incorporated mannan oligosaccharide in *P. monodon* diet observing an increase of THC compared to the control shrimp. A better level of THC and granular hemocyte count was detected in *L. vannamei* when using *S. cerevisiae* as immunostimulants in shrimp diet (Chotikachinda et al. 2008). Babu et al. (2013) used *C. aquaetextoris* as a potential immunostimulant in black tiger shrimp *P. monodon*, observing a reduction in THC after post-challenge with this yeast (Table 2).

Immune defense factors

Many variables, such as total plasma protein content, glucose concentration, alkaline phosphatase activity, clotting time, proPO activity, release of reactive oxygen intermediates, and antibacterial peptide activity (AMPs) have been considered as good health parameters in crustaceans after stimulation with different pathogen-associated molecular patterns (Campa-Córdova et al. 2002; Aguirre-Guzman et al. 2009; Amparyup et al. 2013). Important immune responses in shrimp are phenoloxidase (PO) activity, which is a direct index of defense ability in crustaceans to pathogenic bacteria and viruses. Activation of the proPO system serves an important role as a non-self-recognition system that participates in innate immune responses. It accompanies cellular responses via hemocyte attraction and induces phagocytosis, melanization, cytotoxic reactant production, serine proteinase cascade, particle encapsulation, formation of nodules and capsules (Amparyup et al. 2013). The transformation of proPO to PO activates the production of melanin and toxic reactive intermediates against invading pathogens. Deng et al. (2013) used *S. cerevisiae* (Table 2) in shrimp feed and found that PO and lysozyme activities in serum were significantly higher than the control group, indicating a potential protection against shrimp diseases. Sajeevan et al. (2006) used *F. indicus* diet containing *C. sake* (10%, w/w) and detected a significantly higher immune response in PO activity and nitroblue tetrazolium (NBT), assuming that the immunostimulatory effect of the yeast used in this study helped shrimp survival to experimental WSSV infection (28 days). Lysozyme is capable of degrading gram-negative bacteria cell wall mucopolysaccharides, allowing their recognition by phagocytic cells (Aguirre-Guzman et al. 2009).

Penaeidins are high components of immune response that have antimicrobial and chitin binding properties, which may play an important role in coordination between immune and metamorphosis functions with the synthesis of exoskeleton (Destoumieux et al. 2000). A study showed significant up-regulation of proPO and penaeidin 3a gene expression levels in *L. vannamei* fed the diets supplemented with *S. cerevisiae* products. This study indicated the relevant role of these genes in local immune response, which increased the expression level of penaeidins (Jin et al. 2018). Some penaeidins as crustins, anti-lipopolysaccharide factors and histones play an important role in innate immunity in shrimp (Bartlett et al. 2002; Patat et al. 2004; Somboonwiwat et al. 2005). Biswas et al. (2012) demonstrated a significant stimulation of crustin, lysozyme, and penaeidin gene expressions in the lymphoid organ of *M. japonicus* with the use of *S. cerevisiae* extract (Table 2). Babu et al. (2013) detected similar results when *P. monodon* was fed with diet supplemented with *C. aquaetextoris* at different frequencies pre- and post-challenge to WSSV where crustin 1, 2, and 3, and penaeidin 3, 5 genes up-regulated post-challenge (Table 2).

Bioactive compounds from yeast with immunological effect

Glucans

These molecules are non-specific immunostimulants that induce resistance against bacterial pathogens or used as energy sources. β-glucans are naturally occurring polysaccharides with glucose as structural component, linked by β-glycosidic bonds. Those molecules are active products, administered mainly to shrimp by feed, injection, and orally (Thanardkit et al. 2002; Suphantharika et al. 2003; Aguirre-Guzman et al. 2009; Bai et al. 2014). Yeasts have β-Glucans 50-60 % that are linear or cyclic homopolysaccharides of glucose in their cell wall (Sarlin and Philip 2011; Wilson et al. 2015) linked through β- (1 → 3) and β- (1 → 4) bonds, which can show ramifications (Lazaridou et al. 2007). These molecules in fungi and yeasts are composed of glucose chains with side chains linked by β bonds (1 → 6) (Butt et al. 2008; Volman et al. 2010). The physiological effect of β-glucans depends on its source of origin, dose, structure and molecular weight (Pizarro et al. 2014).

Various studies in shrimp have proven β-glucan as an important immunostimulant for improving immune status and controlling diseases (Sukumaran et al. 2010; Ringø et al. 2012). Glucans are known to invoke various in vivo responses in crustaceans, such as change in hemocyte counts, induction of encapsulation, ProPO activity and melanization, besides generating a range of immunoactive agents including peroxinectin and reactive oxygen species (ROS) (Thanardkit et al. 2002; Suphantharika et al. 2003; Sukumaran et al. 2010; Neto and Nunes 2015). β-glucans are one of the most assuring groups of immunostimulants considered. They have a well-defined chemical structure and mode of action on the immune defense described in a great number of scientific articles (Thanardkit et al. 2002; Felix et al. 2008; Sajeevan et al. 2009a; Bai et al. 2010, 2014; Sukumaran et al. 2010; Zhu and Zhang 2012; Neto and Nunes 2015; Wilson et al. 2015). Immunostimulation potential of eight marine yeast glucans from *C. parapsilosis*, *Hortaea werneckii*, *C. spencermartinsiae*, *C. haemulonii*, *C. oceani*, *D. fabryi*, *D. nepalensis* and *Meyerozyma guilliermondii* were tested against WSSV challenge in *P. monodon* postlarvae (Wilson et al. 2015). Other yeasts used in shrimp (*F. indicus*, *L. vannamei*, *M. japonicus*) that display β-glucans are *C. sake*, *C. tropicalis*, *S. uvarum*, *R. minuta*, *S. cerevisiae* (Table 2). In nature, β-glucans have spread in the cell wall of yeasts, where the shrimp immune system has the ability to detect foreign components, such as LPS and β-glucan present in the cell wall of microorganisms. Specific binding proteins to carbohydrate moieties are found in serum as recognition proteins that activate the cellular functions when they react with the microbial LPS or β-glucan (Aguirre-Guzman et al. 2009). Sajeevan et al. (2009a) and Bai et al. (2014) used β-glucan derivatives from *C. sake* on the immunity of white shrimp *L. vannamei* and *S. cerevisiae* on *F. indicus*, respectively, and its resistance against WSSV. They observed a better resistance in shrimp treated with β-glucan against WSSV and a significant result on immunological parameters [phenoloxidase (PO), respiratory burst, and SOD] and THC.

Nucleotides

In addition to the yeast compounds mentioned, the nucleotide component of the yeast may also contribute to immunostimulation (Sajeevan et al. 2006; Ringø et al. 2012; Subramanian et al. 2014; Xiong et al. 2018). Although most cell types are capable of synthesizing nucleotides from purines and pyrimidines, de novo and salvage synthesis of nucleotides have been thought to be energetically costly. An exogenous source of nucleotides may optimize the functions of rapidly dividing cells, such as those of the immune system that lack the capacity to synthesize nucleotides, so they must depend on a pre-formed source (Ringø et al. 2012). Xiong et al. (2018) studied dietary nucleotide-rich (NT-rich) yeast supplementation in Pacific white shrimp (*L. vannamei*) and reported a significant increase in PO and lysozyme activities in shrimp fed with diet containing 50 g/kg NT-rich. Phenoloxidase (PO) was detected as zymogens in shrimp and displayed a vital role in cell-to-cell communication, cell recognition, and host defense (Lysozyme acts as a first-line defense mechanism to prevent adherence and colonization of microorganisms) (Aguirre-Guzman et al. 2009; Deng et al. 2013). Similar results were obtained by Biswas et al. (2012) with a significant stimulation of crustin, lysozyme, and penaeidin gene expression in the lymphoid organ with the use of NT-rich *S. cerevisiae* extract (Table 2). This stimulation provided resistance to *V. nigripulchritudo* in *M. japonicus.* Guo et al. (2016) used as diet supplement with nucleotide from *K. fragilis* (Rovimax NX) in *L. vannamei*, observing a significant stimulation result of SOD, total nitric oxide synthase and lysozyme.

Effect on water and environmental quality

The intensification process of aquaculture industries had a negative effect on water and sediment quality in shrimp ponds that generate stress to the environment. Yeasts are normal microflora of seawater that are able to improve animal welfare and health by influencing the micro-ecological environment (Deng et al. 2013). The use of some probiotics to face this problem involves manipulation and growth of microorganisms in the ponds to enhance mineralization of organic matter improving water quality and rearing healthier shrimp (Ninawe and Selvin 2009; Silva et al. 2012).

Ammonia is nitrogenous waste, particularly important environmental stress in intensive shrimp farming, causing several physiological changes, including oxygen consumption, homeostasis, and immunosuppression that affect normal growth, health status, and survival rate (Cobo et al. 2014; Thirumurugan and Vignesh 2015). Controlling ammonia in shrimp ponds depends on other quality parameters, such as pH, oxygen, and temperature. The use of *S. cerevisiae* (DV Aqua) indicates a reduction of NH_3-N, chemical oxygen demand and sulphide in water and pond sediment of shrimp culture (*L. vannamei*) (Deng et al. 2013). However, yeast might have acted as probiotic and regulated the microflore sediment, enhancing decomposition of organic matter and undesirable products and reducing the production of toxic gases as suggested by Deng et al. (2013). Furthermore, Melgar et al. (2013) worked with the effect of the commercial natural product composed by (*Rhodopseudomonas palustris*, *Lactobacillus plantarum*, *L. casei* and *S. cerevisiae*) in the culture ponds of *L. vannamei.* This product reduced the total ammoniacal nitrogen and pH water values with positive effect on shrimp growth and survival.

The use of yeast in shrimp farming in the global context

Shrimp aquaculture requires new products, techniques, and strategies to increase production and sustainability. Microorganisms in aquatic animals are a possible tool used in the aquaculture industry; however, knowledge of this field is considerably limited, and yeast is not the exception, especially marine yeast. Yeasts do not work in the same way, this depends on the species or yeast strain, culture medium, product or by-product used, extraction method, and specific application considered (nutrition, immunology, medium environment). The information displayed in this study demonstrated that yeasts play an interesting role for sustainable aquaculture because of their versatile effects on growth, feed efficiency, gut microbiota, immune response besides boosting shrimp resistance against diseases.

Initially, yeast strains used in aquaculture were sub-products obtained for other industries where it was supplied at different levels (1-60% or 1-8 g kg^{-1} shrimp diet). However, yeast displayed interesting results and emerged as alternative feeding ingredients because of their nutritional value (proteins, lipids, vitamins, minerals, etc.) and some bioactive compounds with effect on shrimp growth, survival, digestive system, gut structure, and microbiota interaction. The results have shown the importance of understanding the characteristics of different yeast species/strains in shrimp diet, and their possibility to be used to replace fishmeal with ingredients in balanced feed formula, or additives with effect on shrimp growth, survival, and health. In shrimp, protein digestion is highly efficient and higher protein content usually represents better digestive efficiency, lower conversion ratio and higher survival (Méndez-Martínez et al. 2017). Marine yeasts have been used in the last decades as source of protein, despite of their lack of essential amino acids and high nucleic acid content (Palacios et al. 2007; Alamillo et al. 2017). Consequently, many yeast strains represent today an alternative to partially substitute fish meal in shrimp diet (Alloul et al. 2021). To reduce feed cost, some authors suggest the inclusion of novel protein sources, such as vegetal protein and dried microbial biomass (called microbial protein) in diet of juvenile shrimp as a strategy to maximize the assimilation of low-cost nutrients, improve growth and shrimp production with an animal/vegetal/microbial protein source (Terrazas et al. 2005; Phupet et al. 2018; Alloul et al. 2021).

Several publications have confirmed the beneficial effects of yeasts in shrimp nutrition. These microorganisms synthesized different active products as enzymes, carotenoids product, MOS, etc. which contributed to growth of *F. indicus, L. vannamei*, *P. monodon,* and *P. semisulcatus*. Furthermore, yeasts can be part of the gut microbiota of farmed shrimp where gastrointestinal tract microbiota is important throughout shrimp life and development. Microbiota contributed to feed digestion and nutrient absorption along the gastrointestinal system. The yeast species and their effect on the gastrointestinal tract, enzyme effect or stimulation constituted an important element to study, which has been poorly unextending currently. In addition, evidence has shown that some yeast species/strains have interesting effects on shrimp gastrointestinal health, which is related with shrimp growth, survival, and low stress. Future research with new generation technologies (molecular, proteomic, sequencing) is important to understand the relationship of native microbiota of aquatic animals, microbial ecosystems and with shrimp growth, farming conditions, and environmental factors.

Water quality is a relevant point to understand and control in shrimp industry, especially because the intensification process of shrimp production exhibits degraded conditions and quality of environmental water. Few studies have reported that yeast is used as water quality control, principally for total ammonium control. The use of yeast in water quality and pond sediment is a potential application in aquaculture industry.

Shrimp farming is an important activity in the food sector, which has rapidly developed and intensified, but its growth has displayed an indiscriminate use of veterinary medicines, antibiotics, and chemical products as prophylactic and control measures for pathogens and diseases. This production strategy has resulted in antimicrobial resistance of different pathogens with the risk of spreading. The use of yeast and their products is a possible and viable strategy for prevention and control of diseases to improve the quality and sustainability of aquaculture production. Yeast research with specific active products (glucans, MOS, etc.) apply it in low concentration (<1% kg shrimp diet) and evaluates its effect on target areas of shrimp (hemocytes, hepatopancreas, muscle, etc.). Many studies about yeast cell and their components (inter or extracellular), associated to shrimp production, have reported improved cellular and humoral responses against pathogens (virus, *Vibrio* sp.) and as an efficient strategy to disease prevention/control. Some of these cell compounds activate the shrimp immune response directly, such as phagocytic cells, ProPO system, SOD, antibacterial properties on hemolymph, and mediate signal recognition in cells. In addition, the use of yeast or their active products have been used in shrimp health as anticoagulant proteins, agglutinins, AMPs, antiapoptotic protein encapsulation, bacteriocins, formation of nodules and humoral components, siderophores, gramicidin, polymyxin, tyrotricidin.

The use of appropriate yeast strains, via of administration and dose are necessary for enhancing immune response and to induce resistance against microbial pathogens (Abdel-Tawwab *et al*., 2008; Andrews *et al*., 2011). Yeast stimulants, such as *C. sake* and *C. tropicalis*, are easy to produce and improve the immune system of the Indian white prawn *F. indicus* (Sarlin and Philip 2011). The marine yeast *Y. lipolytica* incorporated at 1.1% in basal diet showed the best feeding method to improve immune response in juvenile shrimp *L. vannamei* (Licona-Jain et al. 2020). Moreover, some studies reported that the mixtures of bacteria and yeast are far more effective for the control of pathogens than single strains, due to the synergic effect of the mix (Peraza-Gómez et al. 2011; Abdel-Rahman and Ahmed 2016; Fierro et al. 2019). More studies testing different marine yeast species (alive or processed) are necessary to broaden the understanding of their action mechanisms and immune response of shrimp species across all developmental stages (embryo, larvae, juvenile, and adult). Thus, specific effect of different yeast species and strains in shrimp immune response is still an important subject of study. Hopefully, new molecular methodologies, such as proteomics, molecular, sequencing, RNA studies will help on this process in the near future.

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Conflict of interest The authors declare that they have no conflict of interest.

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