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REVIEW ARTICLE

Applications of Actinobacteria in aquaculture: prospects and challenges

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Abstract

Disease outbreaks due to improper culture management, poor water quality, and climate change are major concerns in aquaculture. Most of the aquatic pathogens are opportunistic and any imbalance in the host–pathogen-environment triad will result in a disease outbreak. The indiscriminate use of chemotherapeutics such as antibiotics to prevent diseases in aquaculture will lead to antimicrobial resistance in aquaculture. Hence, the demand for natural microbial strains which can be used as beneficial probiotics and bioaugmentors in fish farming systems has increased to ensure one health in aquaculture. Studies have proved the probiotic and bioremediation potential of several Actinobacterial species that can be applied in aquaculture. Actinobacteria, especially *Streptomyces*, can be applied in aquaculture for disease prevention, treatment, and bioremediation of organic and inorganic waste in the culture systems. The growth, immunity, and resistance towards aquatic pathogens in cultured organisms also get enhanced through their capability to release potent antimicrobial compounds, bioactive molecules, and novel enzymes. Their broad-spectrum antimicrobial and quorum quenching activity can be well exploited against quorum sensing biofilm forming aquatic pathogens. Even though they impart specific adverse effects like the production of off-flavour compounds, this could be controlled through proper management strategies. This review discusses the applications, challenges, and prospects of Actinobacteria in aquaculture. Research gaps are also highlighted, which may shed light on the existing complexities and should pave the way for their better understanding and utilisation in aquaculture.

Keywords Actinobacteria · *Streptomyces* · Aquaculture · Probiotic · Bioactive compounds · Bioremediation

Introduction

Aquaculture is considered one of the fastest developing animal farming sectors to cater to the protein demands of the worldwide population (Tal et al. 2009). Disease outbreaks in aquaculture are increasing due to high stocking density, followed by the accumulation of organic and inorganic wastes and diverse microbial infections. Various chemical and biological agents are routinely applied in aquaculture to solve this crisis (Serrano 2005). However, frequent usage of antibiotics and chemotherapeutics leads to their deposition in the aquatic environment and thereby raising multiple antibiotic resistance (Romero et al. 2012; Preena et al. 2020a). Besides, these practices could also suppress the host's immune system (Capkin et al. 2017); hence, alternative methods such as the utilisation of probiotics, and host-associated microbes can be recommended to improve the health of aquatic organisms. Several reports pointed out the importance of microorganisms such as *Bacillus* spp, *Lactobacillus* spp, *Bifidobacterium* spp, *Saccharomyces* spp, *Streptococcus* spp, *Streptomyces* etc. can be used as probiotics and bioaugmentor in aquaculture (Hasan and Banerjee 2020; James et al. 2021; Mugwanya et al. 2022). Among the diverse microbes used in aquaculture, Actinobacteria are reported with multiple applications, such as improvement

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of water quality, immunity, and growth in several aquatic organisms and culture systems (Das et al. 2008a, b; Balagurunathan et al. 2020).

The phylum Actinobacteria consists mainly of 6 major classes, viz. *Actinobacteria, Acidimicrobiia, Coriobacteriia, Nitriliruptoria, Rubrobacteria*, and *Thermoleophilia*. Among the six classes, Actinobacteria are the major group which consists of 15 orders such as *Actinomycetales, Actinopolysporales, Bifidobacteriales, Catenulisporales, Corynebacteriales, Glycomycetales, Jiangellales, Kineosporiales, Micrococcales, Micromonosporales, Propionibacteriales, Pseudonocardiales, Streptomycetales, Streptosporangiales,* and *Frankiales* (Ludwig et al. 2012; Law et al. 2019; Salam et al. 2020). The class Actinobacteria possess unique morphology having Gram-positive bacteria with coccus, rod, and complex fragmenting hyphal morphological features (Miyadoh 1997; Chandra and Chater 2014). Their assorted, extraordinary appearance and close resemblance to fungi were questionable in several situations (Ser et al. 2017).

Actinobacteria usually inhabit soil and marine ecosystems and are found to have noteworthy functions; they play a profound role in biogeochemical cycles, actively involved in bioremediation, production of bacteriocins, and potent bioactive compounds such as novel enzymes and antibiotics (Kurtböke 2017). All these unique and diverse features make Actinobacteria to be explored as an efficient candidate in the aquaculture industry. Their ability to exhibit multiple applications fetched them a new term, "Modern Actinobacteria" (MOD-ACTINO), based on their ability to produce different secondary metabolites (Law et al. 2020). The genus *Streptomyces,* under the order *Streptomycetales* and family *Streptomycetaceae,* is the most well-known and studied Actinobacteria due to their bioactive potentials (Lee et al. 2018). As of the 1970s, around 60% of novel antibiotics were predominantly isolated from *Streptomycetes* (Berdy 2012). Eventually, the researchers unearth the presence of Actinobacteria in diverse environments such as marine, mangroves, deserts, etc., with the expanding endeavours to find new metabolites from different microbial sources. This paved the way for isolating novel Actinobacteria, especially non *Streptomycetes* genera, termed “rare Actinobacteria” with different bioactive potentials (Li et al. 2019; Dhaneesha et al. 2021).

Different probiotic properties of Actinobacteria viz, *Streptomyces*, *Micromonospora, and Salinispora* for aquaculture application were already proven in previous studies (Das et al. 2008a). The potential of Actinobacteria to exhibit antimicrobial action, immune response in fish, growth enhancement, withstanding gut conditions, water quality improvement etc., make it an efficient probiotic (Balagurunathan et al. 2020). Nevertheless, despite the significant features of Actinobacteria, they were least explored as probiotics in aquaculture. Moreover, it is well known that more than 50% of the microbial antibiotics seem to be derived from Actinomycetes, of which *Streptomyces* and *Micromonospora* account for the major compounds (Berdy 2005). Out of the 10,000 antibiotics that emerged from Actinobacteria, they contribute to 45% of all bioactive microbial compounds discovered (Romano et al. 2018). Most of the antibiotics belonging to aminoglycosides, tetracyclines, and macrolides classes, commonly used in aquaculture, are found to be derived from Actinobacteria (Anandan et al. 2016). It is also noteworthy that various members of Actinobacteria were successfully employed in bioremediation (Polti et al. 2014; Rathore et al. 2021). Their unique growth characteristics and diverse metabolic features make them well suited as bioaugmentors in aquaculture.

The efficacy of Actinobacteria in implementing multiple applications prompted us to review their role in the field of aquaculture. Even though different reviews are available in each aspect, the combined potency of Actinobacteria which warrants them to be used as a successful candidate in aquaculture is not discussed so far. The probiotic characteristics of Actinomycetes for aquaculture applications were reviewed in detail previously (Das et al. 2008a; Tan et al. 2016; Balagurunathan et al. 2020). Likewise, the potential features of Actinobacteria in the production of bioactive compounds (Namitha et al. 2021) and other biotechnological products (Jagannathan et al. 2021; Sarkar and Suthindhiran 2022) in performing bioremediation (Rathore et al. 2021) were also documented in earlier reviews (Polti et al. 2014). Due to the scarcity of information available on the multiple features of Actinobacteria in a single review, the current study compiles the comprehensive characteristics of Actinobacteria which can be exploited for aquaculture applications.

Applications of Actinobacteria in aquaculture

As already discussed, Actinobacteria are renowned as a good source of industrially important compounds such as enzymes, antibiotics, anticancer, and antioxidant compounds. Most of these Actinobacterial bioactive compounds can play a vital role in aquaculture. They could be utilised as bioaugmentors, probiotics and feed supplements in aquaculture either individually or as a consortium. Figure 1 depicts the scope of Actinobacteria in aquaculture.

Bioremediation

Water quality deterioration due to the deposition of wastes is one of the major threats in aquaculture for the successful cultivation of finfishes and crustaceans. Organic matter such as feed and the faecal matter settled at the bottom of

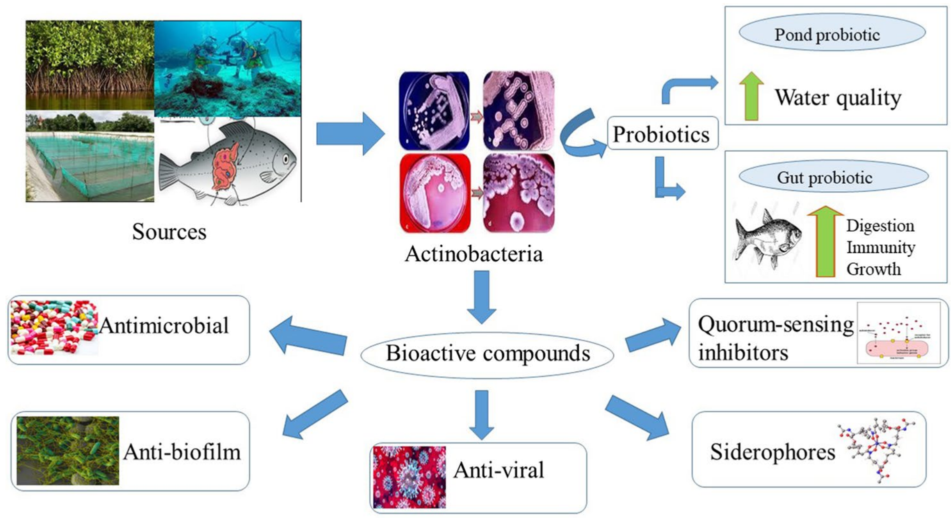

Fig. 1 Significance of Actinobacteria in aquaculture

culture ponds cause deterioration of water quality, thereby affecting the survival of shrimps and other cultured fishes (Avnimelech and Ritvo 2003). Bioremediation is effective in aquaculture for maintaining water quality by applying biostimulants and bioaugmentors. The microbes used for bioremediation involve those which can produce extracellular enzymes that transform complex organic compounds into small ones (Allison and Vitousek 2005). It is already noticed that as compared to Gram-negative bacteria, Gram-positive ones show more bioremediation capacity and convert organic matter into CO_2; this helps to control the build-up of excess carbon in the culture systems (Verschuere et al. 2000). It is advisable to supplement the culture ponds with diverse microbes which can optimise the nitrification, denitrification and carbon mineralisation processes, which helps to reduce the sludge accumulation in culture ponds (Bratvold et al. 1997). Actinomycetes inhabiting both soil and aquatic environments are considered a good source of enzymes such as amylase (Kafilzadeh et al. 2015), cellulase (Maki et al. 2011), chitinase (Gasmi et al. 2019), protease (Gozari et al. 2016), and xylanase (Ninawe et al. 2006), which help in the biotransformation of natural and synthetic matter. The bioremediation potential of Actinobacteria was reported for the first time by Goodfellow and Haynes (1984). Marine Actinobacteria can be effective in the bioremediation of marine pollutants (Rathore et al. 2021). The consortia of Actinomycetes comprising *Streptomyces coelicoflavus*, *S. diastaticus*, *S. parvus*, *S. champavatii* and *Nocardiopsis alba* isolated from marine environments and sediments from shrimp culture pond were found to exhibit good bioaugmentation capability, high hydrolytic enzyme activity and biogranulation property (Babu et al. 2018).

As inorganic compounds are more recalcitrant when compared to organic wastes, it is a major challenge in aquaculture. Actinobacteria gained more attention in degrading both organic and inorganic wastes (Alvarez et al. 2017). The abundance of Actinobacteria in nitrifying and denitrifying bacterial consortia as studied using culture-based and independent methods revealed their efficacy in removing organic and inorganic nitrogenous wastes from aquaculture systems (Preena et al. 2021). The capability of Actinomycetes in performing nitrification (Hirsch et al. 1961) and denitrification (Shoun et al. 1998) is reported in very earlier period onwards. This combined nitrifying and denitrifying capability of Actinobacteria makes it a suitable bioaugmentor in aquaculture. The complete removal of inorganic nitrogen to N_2 was reported in *S. antibioticus* for the first time by Kumon et al. (2002). This complete denitrification eliminates the risk of toxic nitrate accumulation in the system. Aerobic denitrification was also reported in *Streptomyces* strains from wastewater plants (Zhang et al. 2021) and in *S. tendae* and *S. enissocaesilis* from nitrifying bacterial consortia for establishing nitrification–denitrification in shrimp larval rearing systems (Preena et al. 2017). This highlighted the simultaneous occurrence of nitrification and denitrification even under oxygenated conditions, eliminating the requirement of any extra compartment or carbon sources for denitrification. In addition, culture-independent methods also corroborated the abundance of Actinomycetales (10%) within the nitrite oxidising consortia (Preena et al. 2018) and 18% in the ammonia oxidising consortium (Preena et al. 2019). The coexistence of Actinobacteria with autotrophic nitrifiers and heterotrophic denitrifiers highlighted the contribution of Actinobacteria in providing necessary signals to the functional communities to perform nitrification–denitrification. Besides, Actinobacteria such as *Streptomyces roseoflavus* and *S. thermocarboxydus* were identified as the dominant taxa among several biofilter communities in recirculating aquaculture systems (RAS) (Schreier et al. 2010; Bartelme et al. 2017). The taxonomic composition of the marine drum and trickling nitrification filter was found to be enriched with *Streptomyces roseoflavus* and *S. thermocarboxydus* (Schreier et al. 2010). Their increased existence in biofilters associated with RAS brings out their significance in waste removal. Marine Actinomycetes such as *S. parvus, S. rochei, S. griseorubens, S. griseus and S. albidoflavus*, were efficiently found to remove ortho phosphates and ammonia from domestic wastewater (Madkour et al. 2019).

The tremendous potential of Actinobacteria to degrade organic contaminants could be exploited for the cleaning up of contaminated aquaculture environments. *Streptomycetes* and *Micromonospora* spp. have shown to be the better hydrocarbon degrading microbes (George et al. 2011). Their biosurfactant production property for hydrocarbon degradation is also noteworthy. Khopade et al. (2012) demonstrated the production of biosurfactants in large quantities by marine *Streptomyces* spp. Because of the efficacy under extreme conditions (salinity, pH, temperature), bioemulsifiers produced by Actinobacteria can be widely employed in fresh brackish and marine culture systems for waste degradation (Selim et al. 2021). Nevertheless, marine Actinomycetes are least studied for biosurfactant production. Actinobacterial groups having potential in bioremediation, biosurfactant production and hydrocarbon biodegradation can be applied individually or as a consortium in aquaculture systems for waste removal.

Bioactive compounds

Actinomycetes serve as an important source of commercially as well as medically important bioactive compounds (Takizawa et al. 1993; Jagannathan et al. 2021). Marine Actinobacteria are considered one of the main sources of bioactive compounds. *Streptomyces*, *Micromonospora,* and *Salinispora* are the significant Actinobacterial groups that produce several bioactive compounds (Selvameenal et al. 2009; Lee et al. 2014a; Amin et al. 2020). The main bioactive compounds include various antibiotics, antifungal, antitumor, antiparasitic and immunosuppressive agents, and various enzymes (Lee et al. 2014b).

Actinomycetes have been screened from diverse niches of the marine environment, such as deep sea, seaweeds, mangroves, and seagrasses (Barcina et al. 1987; Jensen et al. 1991; Weyland and Helmke 1998; Urakawa et al. 1999). One of the important bioactive compounds produced by Actinobacteria is antibiotics. Around 80% of global antibiotics are reported from Actinobacteria, especially from the genera *Streptomyces* and *Micromonospora* (Anandan et al. 2016). Based on structure, the antibiotics produced by Actinobacteria are classified into different types such as aminoglycosides, ansamycins, anthracyclines, β-lactam, macrolides and tetracycline (Amin et al. 2020). *Streptomyces* isolated from seagrass was found to be a potent antibiotic producer that displayed antagonistic activity against fish, shrimp and human pathogens (Ravikumar et al. 2012). You et al. (2005) successfully isolated various strains of Actinobacteria from sediments of a shrimp farm, of which 87% represent *Streptomyces* followed by *Micromonospora.* They also exhibited antagonistic activity against the major shrimp pathogen, *Vibrio* and also possessed siderophore production, which in turn helps to decompose organic compounds such as starch, protein and cellulose. Siderophore producing Actinobacteria could also eliminate the existence of major aquatic pathogens by competing for iron, an essential element for growth and biofilm formation, and hence this could be a promising candidate as a biocontrol agent and good bioremediator in aquaculture systems (You et al. 2005). Besides, most of the *Streptomyces* strains segregated from marine samples also exhibited antimicrobial activity against *Aeromonas hydrophila*, *A. sobria* and *Edwardsiella tarda* (Patil et al. 2001). Also, *Streptomyces* associated with marine sponges exhibited antagonism against *Aeromonas hydrophila*, *Serratia* spp., and *Vibrio* spp. through the production of polyene substances (Selvakumar 2010). Almost all virulent species of *Vibrio* such as *V. Parahemolyticus, V. alginolyticus* and *V harveyi* were found to be sensitive towards most of the soil Actinobacteria isolates (Nabila et al. 2018). This highlights the significance of the application of Actinobacteria in shrimp culture systems. Recently, a novel species, *S. virginiae* isolated from the soil, exhibited wide-spectrum bacteriostatic activity against several fish pathogens and increased the resistance of goldfish (*C. auratus*) against *A. veronii* (Hu et al. 2021). In addition to the antagonistic property, the Actinobacteria also improve the growth in cultured organisms (Dharmaraj and Dhevendaran 2010).

It is well known that the persistence of *Vibrio* spp. in shrimp and fish farms leads to the development of antibiotic-resistant biofilms, which badly affects shrimp and fish growth and survival (Karunasagar et al. 1994; 1996). The application of bioactive extracts from marine Actinomycetes, especially the multifunctional strain *Streptomyces albus*, inhibited the biofilm formation of *Vibrio harveyi, V. vulnificus, and V. anguillarum*, and the extracts displayed efficient clearance of mature biofilm (You et al. 2007). The extracts exhibited quorum-sensing inhibition activity by attenuating the activity of signal molecules, N-acylated homoserine lactone in *Vibrio* spp. Gut-associated Actinobacteria from two marine fishes such as Indian mackerel and Panna croaker proved their potential to develop novel therapeutic drugs by exhibiting antimicrobial and quorum quenching activity towards significant aquatic pathogens (Vignesh et al. 2019). Promising inhibitory activity of Actinomycetes against the biofilm structure of aquatic pathogens like *A. hydrophila, Vibrio harveyi, and Streptococcus agalactiae* again highlighted their quorum quenching activity (Raissa et al. 2020).

Even though reports of antiviral compounds from Actinobacteria are less, bioactive extracts (guanine7-N-oxide) from *Streptomyces* were found to inhibit fish pathogens such as Infectious Pancreatic necrosis Virus, Infectious Hematopoietic Virus and fish Herpes Virus as evident in an earlier study (Hasobe and Saneyoshi 1985). The bioactive compounds derived from Actinobacteria possess significant antimicrobial activity against a major shrimp pathogen, the white spot syndrome virus (Kumar et al. 2006; Namitha et al. 2021). The *Litopenaeus vannamei* infected with WSSV on treatment with ethyl acetate extract of bioactive compound 9(10H)-acridanone from *S. fradiae* strain at a concentration of 500 mg/animal exhibited a survival rate of 83.3% (Manimaran et al. 2018). Ethyl extracts of benzoic acid metabolites isolated from marine *Streptomyces castaneoglobisporus* have displayed antibacterial, antifungal and antiviral activity (Jenifer et al. 2018). These derivatives inhibit bacterial multiplication by inhibiting cell wall synthesis, translation and transcription and viral transcription through their interaction with the outer and nucleocapsid proteins. *Streptomyces griseus, S. fradiae, S. flavidofuscus, Nocardia nova* and *Brevibacterium linens* also exhibited inhibition against WSSV in *Penaeus monodon* (Nair et al. 2012). The growth of toxic algae (*Phaeocystis globosa*) in eutrophic ponds was also found to be removed using marine *Streptomyces* spp. (Zhang et al. 2015). This highlights the broad-spectrum action of bioactive molecules derived from Actinobacteria against bacteria, biofilms, virus and algae and thus overcome the challenges raised by chemically synthesised narrow spectrum antibiotics.

Probiotics

The frequent usage of antibiotics to control pathogens could lead to the proliferation of antibiotic-resistant bacteria due to selection pressure, which may then exchange their resistance genes with animal and human pathogens through mobile genetic elements (Jagannathan et al. 2021). The emergence of antimicrobial resistance in the dominant fish pathogen such as Vibrio is of major concern (Beaz-Hidalgo et al. 2010). Increased occurrence of antimicrobial resistant aeromonads and enterobacteraceae groups with plasmid borne antibiotic resistant genes were reported from various aquaculture farms, highlighting the possibility of AMR spread through horizontal gene transfer (HGT) (Preena et al. 2020b, c). Hence alternative strategies like the application of probiotics and immunostimulants are significant in regulating diseases in aquaculture (Qi et al. 2009). The mechanism by which probiotics suppress fish pathogens includes mainly bacteriocin production, quorum quenching activity and competitive exclusion (competition for attachment sites and nutrients) (James et al. 2021). A good probiont should be adherent to the intestinal tract, fast multiplying, secrete antimicrobial compounds and withstand acidic environments (Das et al. 2008b). Microbes such as *Bacillus*, *Lactobacillus*, *Pseudomonas* and *Burkholderia* are the common microbes that are frequently used as aquatic probiotics (Kesarcodi-Watson et al. 2008; Luis-Villaseñor et al. 2013; Knipe et al. 2021). Meanwhile, in search of a novel potent probiotic strain, diverse Actinobacteria groups were found to synthesise several efficient chemical compounds to combat various pathogens. The characteristics of Actinomycetes as probiotics are attributed to their ability to synthesise amylase, protease, lipase and other enzymes, which aid in the absorption and digestion of nutrients in the host (Jagannathan et al. 2021). In a recent study, Actinobacteria isolated from fish guts displayed enhanced immunity and pathogen resistance (Thejaswini et al. 2022). This underlines the improved performance of host-associated microbes compared to other terrestrial niches (Van Doan et al. 2018). The overall growth performance and effective disease control were found to be upregulated in shrimps and fish by incorporating Actinobacteria in feed (Tan et al. 2016). Table 1 lists different types of Actinobacteria, which are used as probiotics and their application in aquaculture.

Gut probiotics

The growth of post larval *P. monodon* improved after feed supplementation with mangrove sediment isolate *Streptomyces fradiae* (Aftabuddin et al. 2013). The feeds supplemented with *Streptomyces* displayed improved growth and FCR in ornamental fish, *Xiphophorus helleri* (red swordtail fish) (Dharmaraj and Dhevendaran 2010). Actinobacteria isolated from faecal samples of chicken showed higher pH, pepsin, bile and pancreatin resistance and were found to be the ideal choice as gut probiotics in animals because of their higher colonising and adapting nature in the gastrointestinal tract (Latha et al. 2015). This is in close agreement with a previous study, where *Streptomyces* strains isolated from shrimp pond sediment displayed fast adaptation and active existence in the digestive system of shrimp even in the presence of bile acids and a low pH environment (Das et al. 2010). The use of these *Streptomyces* probiotics provides effective protection against vibrio pathogens in both juvenile and adult artemia. Das et al. (2010) reported improved survival rate in artemia after being challenged with vibrio pathogens (*V. harveyi and V. proteolyticus*) and increased weight in cultured shrimps (*Penaeus monodon*) was observed when bioencapsulated probiotic feed of *Streptomyces* administered to them. This underlines the secretion of hydrolytic exoenzymes by *Streptomyces* spp., which augmented the amylolytic and proteolytic activity in the shrimp digestive tract for better utilisation of feed. The bioactivity of marine Actinomycetes from the sediments of Caspian Sea was remarkable

Table 1 Actinobacterial probiotics used in aquaculture systems

Sl.No	Probiotic	Method of administration	Culture organism	Outcome	References
1	*Streptomyces*	SCP	Shrimp and young prawn	Increased development and protein content and feed conversion efficiency	Nakamura et al. (1977)
2	*Streptomyces*	SCP	Shrimp	Sources of protein	Manju and Dhevendaran (1997)
3	*Streptomyces olivaceogriseus*	Injection	Rainbow trout	Significant growth and resistance against *Aeromonas salmonicida* and *Yersinia ruckeri*	Sakai (1999)
4	*Streptomyces*	Feed	*Penaeus monodon*	Weight gain and improved digestion	Das et al. (2010)
5	*Streptomyces*	Feed	*Xiphophorus helleri*	Improved growth	Dharmaraj and Dhevendaran (2010)
6	*Streptomyces fradiae*	Feed	*Penaeus monodon*	Increased growth	Aftabuddin et al. (2013)
7	*S. rubrolavendulae*	Bio-granules	*Penaeus monodon*	Antagonistic activity against the vibrio sp	Augustine et al. (2015)
8	*Streptomyces and Bacillus*	Feed	*Shrimp*	increased haemocyte production, higher survival growth rate and protection against vibrios	Bernal et al. (2015)
9	*Streptomyces coelicoflavus*, *Streptomyces diastaticus*, *Nocardiopsis alba*, *Streptomyces parvus* and *Streptomyces champavatii*	Added to rearing water	*Penaeus monodon*	Improved water quality parameters and growth performance	Babu et al. (2018)
10	EM.1® (lactic acid bacteria, photosynthetic bacteria, yeasts and Actinomycetes)	Added to rearing water	Nile tilapia	Improved water quality parameters and growth performance	Bahnasawy et al. (2019)
11	*Streptomyces*	Feed	*Litopenaus vannamei*	Stimulation of gut microbiota and protection against *V. parahaemolyticus*	Mazón-Suástegui et al. (2020)
12	*Nocardiopsis alba*	Feed	*Penaeus monodon*	improving immunity, growth and protection from vibriosis	Sunish et al. (2020)
13	*S.amritsarensis*	Feed	Grass carps	Antagonism against fresh water fish pathogens and enhances the growth and disease resistance	Li et al. (2020)
14	*Streptomyces antibioticus*	Feed	*Freshwater catfish*	Enhanced growth and feed intake, nutrient digestibility and survibality, protection against fish pathogens like *Aeromonas veronii* and *Stenotrophomonas maltophilia*	Das et al. (2021)

for probiotic potential by possessing antagonism against multi drug resistant vibrios (Norouzi et al. 2018). The probiotic potential of Actinomycetes can be enhanced through the combined application with other bacteria (Jagannathan et al. 2021). An increased haemocyte production, higher survival, growth rate and protection against vibrios were observed in shrimps when *Streptomyces-Bacillus* combined feed was given (Bernal et al. 2015). While in another study, compared to *Bacillus cereus, Streptomyces antibioticus* isolated from the gut of vermicomposting earthworm was noticed as an excellent protein source to juvenile catfish by providing significant nutrient digestibility and utilisation, overall growth performance and survivability and protection against fish pathogens like *Aeromonas veronii* and *Stenotrophomonas maltophilia* (Das et al. 2021). Survival in an acidic and alkaline environment, extracellular enzymatic action, hydrophobicity towards solvents and increased tolerance to gastric juice and bile salt are the notable probiotic features of those Actinomycetes. Recently, a new strain, *S. amritsarensis* was successfully applied as probiotic in freshwater fish aquaculture for the first time (Li et al. 2020). It was noticed to have broad spectrum antibacterial action towards freshwater fish pathogens and enhances the growth and disease resistance of grass carps. The application of *Streptomyces* probiotics was also found to improve the gut microbiota of *Litopenaus vannamei* by increasing the bacterial diversity, stimulating the bacteriovorax population and antibiotic producing genera and thereby protecting against vibrios (Mazón-Suástegui et al. 2020).

Immunostimulants

Activation of the immune system in farmed fish and shrimp employing immunostimulants is common in aquaculture as a part of disease prevention. Actinomycetes also take part in providing effective immunoactive peptides to boost immunity in fish and shrimps. Most of the bioactive compounds that emerged from Actinobacteria could be administered either orally or by injection in fish as immunostimulants to enhance their immunity and growth performance (Namitha et al. 2021). *Streptomyces olivaceogriseus* was reported to secrete lactoyltetrapeptide (FK-156) which could induce resistance against major pathogens like *Aeromonas salmonicida* and *Yersinia ruckeri* in rainbow trout (Sakai 1999). A marine Actinomycete *Nocardiopsis alba* exhibited good immune modulatory activity in tiger shrimp *P. monodon* by improving immunity, growth and protection from vibriosis (Sunish et al. 2020). Phenoloxidase, respiratory burst, total protein, acid and alkaline phosphatases were seen to be elevated and upregulation of various immune genes such as *alpha 2 macroglobulin, penaeidin − 3, transglutaminase, proPO, crustin* and *peroxinectin* were observed in those fed with Actinomycetes.

Single cell protein

The dwindling resources of fishmeal necessitate the search for alternative protein sources and the single cell protein (SCP) of Actinobacterial origin can replace about 25–50% of fishmeal in aquafeeds (Selim et al. 2021). Secondary metabolites such as aplasomycin, boromycin and regular amino acids like azaleucine and alanosine produced by *Streptomyces* enable them an ideal choice for SCP production (Berdy et al. 2012). The use of *Streptomyces* as SCP has increased in recent years because of the advantageous effects such as improved feed conversion, enhanced growth of aquatic organisms and low cost of production and maintenance (Manju and Dhevendaran 1997; Selvakumar et al. 2013). As evident in an earlier study, Actinomycete incorporated feed elevated the rate of development, protein content and feed conversion efficiency in shrimps and young prawns (Nakamura et al. 1977).

Pond probiotics

As already discussed, maintenance of water quality is one of the major constraints in aquaculture as increased ammonia and nitrite level badly affects the health of cultured aquatic organisms. The usage of pond probiotics could resolve the issue to a great extent. Pond probiotics not only improve the water quality of pond water but also help to improve the immunity and growth of cultured fishes. The enzymatic digestion, sonic vibration and resistant spore producing abilities of these microbes help them to survive and sustain in extreme environmental conditions, and it also improves their shelf life in aquatic ponds (McBride and Ensign 1987). Actinobacteria especially *Streptomyces* spp. applied as pond probiotics was found to reduce the ammonia level and increase the heterotrophic microbes in the water bodies as well (Aftabuddin et al. 2013). *Streptomyces panacagri* and *Streptomyces flocculus* had shown antagonistic activity against *Vibrio harveyi*, *Vibrio parahaemolyticus* and *Vibrio vulnificus* and also possessed various extracellular enzymatic activities and high degradation potential (Bernal et al. 2015). The application of these strains as such in brackish systems helped to improve the growth of aquatic organisms as well as the water quality through bioremediation. The use of commercial probiotic EM.1® comprising 80 species of microorganisms containing lactic acid bacteria, photosynthetic bacteria, yeasts and Actinomycetes showed significant improvement in fish productivity and water quality. The probiotic addition at 200 ppm in rearing water positively affects the chemical composition of whole-body fish by increasing food conversion ratio (1.49 ± 0.07) and protein content (13.85 ± 0.21), increases dissolved oxygen level (9.02 ± 0.48 mg/l), decreases ionised ammonia (0.77 ± 0.03 mg/l) and unionised ammonia

(0.04 ± 0.01 mg/l) (Bahnasawy et al. 2019). Pond probiotics thus simultaneously act as bioaugmentors for waste removal and immunostimulants for fish health in the open and closed cultured systems. A marine Actinomycete, *Streptomyces rubrolavendulae* when applied as biogranules in *P. monodon* postlarval rearing system, an increased *in-vivo* exclusion of *V. harveyi, V. alginolyticus, V. parahaemolyticus* and *V. fluvialis* was recorded in shrimps (Augustine et al. 2016). Thus, the treatment of culture systems with Actinomycete biogranules is also a better option to provide *in-vivo* protection in shrimps against vibriosis.

Challenges and prospects of Actinobacteria in aquaculture

Compared to other Gram-positive probiotics, Actinobacteria are difficult to culture because of the slow growth rate, complexities in isolation and identification and cross contamination (Das et al. 2008a). The existence of various antibiotic resistance genes (ARG) viz. efflux pumps, modifying enzymes and ribosomal protection proteins within Actinomycetes for their protection is another challenge. Meanwhile, since horizontal gene transfer could happen in any of the environmental strains, probiotic strains need not be the reservoir, which may contribute to the major AMR spread (Das et al. 2008b). This is strengthened by the fact that most of the antimicrobial resistance incidence is reported in aquaculture, where the vast application of antibiotics occurs rather than HGT (Preena et al. 2020a). Another advantage is that the plasmid in Actinomycetes is linear and incompatible with other phyla; the possibility of ARG spread through lateral gene transfer is rare (Jagannathan et al. 2021). Nevertheless, the possible risk in the mobility of antibiotic resistance genes in Actinobacterial strains should be assessed before application in aquaculture (Tan et al. 2016).

Production and accumulation of compounds such as geosmin and 2-methylisoborneol (MIB) in Actinobacteria can cause off-flavour in fishes (Smith et al. 2008). This creates unwanted earthy or musty flavour, which may badly affect the quality of aquatic organisms; hence their detection and elimination are essential. The production of these terpenoid compounds in freshwater aquaculture, and recirculating aquaculture creates awareness earlier (Das et al. 2008b). The fish quality gets reduced by the entry of these compounds through the skin, gills and gastrointestinal tract, thereby diminishing the commodity value (Howgate 2004). Among the Actinobacteria, *Streptomyces* play a lead role in odour formation (Schrader and Summerfelt 2010). However, other than Actinomycetes, Cyanobacteria, other bacteria and fungi also play a significant role in the production of these off-odour compounds in the aquaculture systems (Wood et al. 2001). Hence the Actinobacteria groups alone are not responsible for this crisis, and their restricted use as probiotic does not solve this particular issue. The abundance of these compounds in the cultured system can be monitored through quantitative PCR and gas chromatography e mass spectrometry (GCeMS) (Auffret et al. 2011). Several efforts involving ozonation, biofiltration, depuration and use of powdered activated carbon could successfully remove these odorants from aquaculture systems (Tan et al. 2016).

Even though reports are rare regarding the Actinobacterial infection in aquaculture, nocardiosis, caused by *Nocardia* spp. has been reported in some of the cultured fishes (Matsumoto et al. 2016; Brosnahan et al. 2017). *Nocardia seriolae* is the most often detected species in diseased fish (Nayak and Nakanishi 2016). Hence, proper pathogenicity studies should be conducted before commercialising the Actinobacterial probiotic in aquaculture.

Research gaps

Actinobacteria act as a significant hotspot for novel bioactive metabolites like wide spectrum antibacterial, antiviral, anti-biofilm, anti-quorum sensing, antifungal and antiparasitic activity. Even though their potential activity against human pathogens is elaborately studied, efficacy against fish pathogens needs further research. As discussed in the previous section, many Actinobacterial bioactive molecules reported antiviral activity against WSSV. However, the broad-spectrum antiviral property of marine Actinobacteria (Raveh et al. 2013) were least exploited against fish and shrimp viral pathogens. Parasitic infestations due to *Diptera, Oligochaeta, Ostracoda*, etc., are increasing in aquaculture (Paladini et al. 2017), especially in cage culture due to the poor water quality and global warming (Nowak 2007). Fungal diseases like branchiomycosis, saprolegniasis and ichthyophoniasis are also not uncommon in aquaculture (Choudhury et al. 2014). Though numerous antiparasitic (Dhanasekaran et al. 2012) and antifungal (Selim et al. 2021) secondary metabolites were reported to be derived from marine Actinobacteria, they were scarcely tested in aquaculture system. The quorum quenching potential of Actinobacteria can also be well utilised to mitigate the multidrug-resistant vibrios in marine and brackish aquaculture systems. Besides, several members of Actinobacteria such as *Streptomyces, Micromonospora, Nocardia, Nocardiopsis* etc. are also well known for antimicrobial peptide (AMPs) synthesis for exhibiting broad-spectrum antimicrobial activity (Joseph et al. 2021). However, the AMPs from Actinobacteria were hardly employed in aquaculture systems, which paved the way for further studies.

The vast diversity of marine actinobacteria is underexplored for their novel metabolite production (Anandan et al. 2016). Future research should also focus on marine and brackish water fish gut Actinobacteria since the recent studies retrieved novel bioactive molecules from the significantly diverse Actinobacteria from the fish gut (Jami et al. 2015; Thejaswini et al. 2022; Shijila et al. 2022). The existence of Actinobacteria in fish gut highlights the scope of using even prebiotics in the cultured systems to improve the probiotic potential of Actinobacteria already inhabiting the gut microbiome. In addition, since Actinobacteria serve as the niche for enzymes responsible for both probiotic and prebiotic production (Das et al. 2008b), the synbiotic approach (combination of probiotics and prebiotics derived from Actinobacteria) can also be taken into consideration in aquaculture.

Necessary steps can also be initiated to establish consortia comprising efficient Actinobacterial groups for the activation of various aquaculture-based systems. Such kind of consortia developed through enrichment techniques can be applied in either encapsulated forms or as biogranules. The effect of Actinobacteria on other beneficial microbes used in aquaculture systems needs further research. Though concerns exist in isolation, off flavour compounds, their excellence in offering remarkable bioactive compounds, probiotic potential and bioaugmentation capability warrants the application of Actinobacteria in aquaculture for disease management and improved production.

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Data availability All data related to this study are included in the manuscript.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest. The authors declare no competing interests.

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