



Biological strategies in aquaculture disease management: Towards a sustainable blue revolution

Keng Chin Lim^{a,b}, Fatimah Md Yusoff^{a,b,c}, Fatin M.I. Natrah^{a,c}, Mahanama De Zoysa^d, Ina Salwany Md Yasin^{a,c}, Jasmin Yaminudin^a, Murni Karim^{a,b,e,*}

^a Department of Aquaculture, Faculty of Agriculture, Universiti Putra Malaysia, UPM, 43400, Serdang, Selangor, Malaysia

^b International Institute of Aquaculture and Aquatic Sciences, Universiti Putra Malaysia, 71050, Port Dickson, Negeri Sembilan, Malaysia

^c Institute of Bioscience, Universiti Putra Malaysia, UPM, 43400, Serdang, Selangor, Malaysia

^d College of Veterinary Medicine and Research Institute of Veterinary Medicine, Chungnam National University, Daejeon, 34134, Republic of Korea

^e Department of Aquaculture, Faculty of Fisheries and Marine, Universitas Airlangga, Campus C, Surabaya, 60115, Indonesia

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ABSTRACT

Although the aquaculture industry has undergone monumental development worldwide, the ever-present threats of infectious diseases have become a constraining factor, imperiling its sustainability. Antimicrobial resistance (AMR) remains a real menace to industrial aquaculture due to the careless adoption of preventive therapies (antimicrobial therapeutic drugs) to forestall disease outbreaks in aquatic food production. Suitable strategies, or at least supplementary measures, should therefore be developed to curb the emergence and widespread transmission of AMR. Vaccination represents one of the primary options to substantially mitigate the economic damages imposed by emerging infectious diseases on global aquaculture; nevertheless, the availability of commercial aquatic vaccines is usually limited, and many vaccines only confer minimal or poor protection against infections (during the early stages of animal development). Accordingly, a large body of research has been enthusiastically exploring alternate approaches for managing animal health challenges. These efforts have led to the establishment of various biocontrol strategies, such as the versatile use of high-value functional ingredients (e.g., probiotics, prebiotics, synbiotics, paraprobiotics, postbiotics, and phytochemicals), phage therapy, and quorum-sensing interference (QSI), to promote the health and welfare of farmed aquatic species in a responsive or preventative manner. This review article addresses the state-of-the-art pertinent to biological control as an eco-friendly green approach for aquatic disease management, paving the route to a sustainable blue revolution. The potential biological mechanisms of these strategies are also described, along with the impediments to scientific progress and topics that merit further investigation.

1. Introduction

Aquaculture production holds immense potential for contributing to human nutrition and health, as wild stocks have dwindled vastly due to overexploitation, habitat change, and pollution. Persistence in reliance on capture fisheries does not seem to be a sustainable alternative, and aquaculture has been granted top priority in this respect. The 2024 edition of *The State of World Fisheries and Aquaculture* (SOFIA) reported that global fisheries and aquaculture production reached 223.2 million tonnes in 2022, marking a 4.4 % increase from 2020. This total included 185.4 million tonnes of aquatic animals and 37.8 million tonnes of

algae. Along with the surging world population and growing food demand, total aquaculture production is anticipated to expand swiftly towards 2030 while remaining one of the most lucrative areas of the food industry (FAO, 2022). The record production of aquatic foods highlights the sector's potential in addressing food insecurity and malnutrition. In 2021, global apparent consumption of aquatic animal foods reached 162.5 million tonnes. Since 1961, this figure has grown at nearly twice the rate of the world population, with annual per capita consumption increasing from 9.1 kg in 1961 to 20.7 kg in 2022 (FAO, 2022). Nevertheless, the intensification and globalization of the aquaculture industry have been plagued by infectious diseases (both

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* Corresponding author. Department of Aquaculture, Faculty of Agriculture, Universiti Putra Malaysia, UPM, 43400, Serdang, Selangor, Malaysia.

E-mail address: murnimarlina@upm.edu.my (M. Karim).

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emerging and reemerging), posing major challenges to the sector. Extensive and intensive farming practices radically alter the ecology of cultured animals, particularly during stressful circumstances (e.g., overcrowding, poor water conditions, and environmental deterioration) that evoke the emergence and spread of infections, resulting in eventual production collapse, severe economic losses, and jeopardizing the sustainability of the industry altogether. The outbreak of infectious diseases in aquaculture was recognized as the principal cause of production losses in the questionnaire for the Census of Aquaculture 2018, undertaken by the United States Department of Agriculture (USDA) (FAO, 2022; Lim et al., 2023). The World Bank reports that aquaculture diseases entail an estimated economic damage of USD 6 billion yearly on a global scale (Cain, 2022; Lim et al., 2023). Moreover, the adverse impacts of the routinely applied or overused therapeutic and prophylactic agents (antimicrobials) to mitigate disease burdens, which could end up in the environment and aquatic products (as residues or degradation byproducts), are a primary concern with reference to AMR and potential human and animal health risks (Barnes et al., 2022; Barnes et al., 2022; Prabina et al., 2023; Wang et al., 2023; Zhang, Yang, Eggermont, & Defoirdt, 2023). Antimicrobial resistance is projected to cause 10 million human fatalities by 2050, while the World Bank estimates that AMR could trigger a 3.8 % economic loss by 2050 (Frei et al., 2023; Kumari et al., 2023; Murray et al., 2022). Alternatively, vaccination has been eagerly embraced as a way out; however, the effectiveness is usually limited or unsatisfactory when applied during the early developmental stages of aquatic animals due to their low overall core capacity for immunocompetence (immature immune system) (i.e., fish fry and fingerlings) and also the inarguably less developed adaptive or acquired immune responses in some species (i.e., crustaceans and mollusks) (Kumar et al., 2022; Marana et al., 2022; Pereira et al., 2022; Robinson et al., 2023). These animals are, undoubtedly, most vulnerable to a wide range of diseases during their early life stages, when they may not be fully immunocompetent. Besides, the development of new vaccines for aquaculture can be costly and impractical (Micuchova et al., 2022; Pereira et al., 2022). Consequently, disease prevention and successful health management are among the most critical facets of sustainable and thriving aquaculture production.

The ominous AMR phenomenon warrants prompt measures via the development and timely adoption of alternative approaches to preserve the quality while assuring the safety of aquatic products. Against this background, researchers across the world have been engaged in continual efforts toward the biological management of aquatic diseases with the constant incorporation of new knowledge and techniques. The concept of biological control centers on any sort of biological manipulation of the host, the environment, and the pathogens (or diseases) intended to control or prevent infection. A wide array of biocontrol strategies, including the promising applications of functional ingredients (e.g., probiotics, prebiotics, synbiotics, paraprobiotics, postbiotics, and phytochemicals) (Yusoff et al., 2020; Zabidi et al., 2021; Alvanou et al., 2023; Butt et al., 2023; del Valle et al., 2023; Lim et al., 2023), phage therapy (Liu, Han, et al., 2022; Lomeli-Ortega, Balcazar, & Quiroz-Guzman, 2023), and QSI (Gupta & Kumar, 2022; Guzman et al., 2022; Zhu, Chen, et al., 2023), have been explored broadly (Fig. 1). High-performing functional ingredients continue to gain traction universally, with numerous health benefits to terrestrial and aquatic organisms beyond enriching nutrition, owing to their nutraceutical benefits. These bioactive components are linked to the prevention of nutrient deficiency, superior gut function, bolstered intermediary metabolism, growth promotion, enhanced stress tolerance and immunity, as well as protection against diseases (Abdel-Latif et al., 2023a; Lim et al., 2018; Lim et al., 2019, 2021, 2023; Lim, Yusoff, Shariff, & Kamarudin, 2021; Lim et al., 2023). Of late, with the escalation of the AMR crisis, phage therapy is experiencing a well-deserved revitalization as a multi-dimensional strategy to battle infectious agents in aquaculture, with high specificity and efficiency (Lomeli-Ortega, Barajas-Sandoval et al., 2023; Pereira et al., 2022). To further restrict the usage of

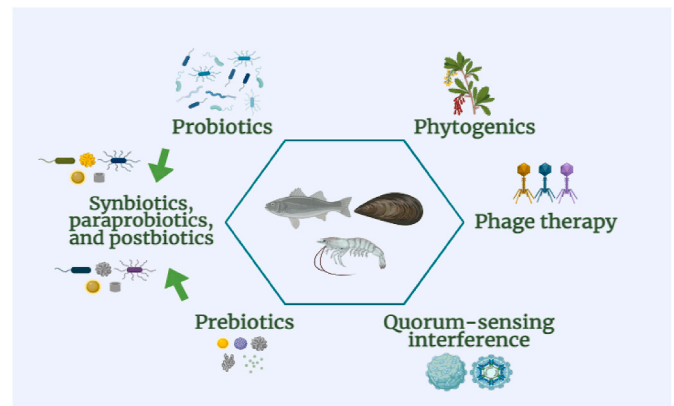


Fig. 1. Biological control strategies for aquaculture health management.

antimicrobials, QSI has been comprehensively investigated in recent years as a novel antivirulence therapy to disarm pathogens, thereby limiting their pathogenicity while preventing infection (Saeki et al., 2020; Zhu, Chen, et al., 2023). Given the quest for viable substitutes, biological approaches could be deemed a sustainable option for health management in aquaculture.

Current advancements in genetic engineering, metabolomics, metagenomics, metatranscriptomics, and synthetic biology have inspired newfound enthusiasm and novel explorations that have further revolutionized the field (Cruz et al., 2022; Lim et al., 2023; Liu, Han, et al., 2022; Strathdee et al., 2023; Zhu, Chen, et al., 2023). This has truly motivated funding agencies or organizations to support a series of experimental trials as well as investments from biotech start-ups. Although research on biological control agents in aquaculture has built immense momentum through the years, the information remains poorly assembled as a whole. It is imperative, however, to integrate the information so that the implications and outcomes are focalized. The present review is an informative compilation of the various biological strategies for disease control in aquaculture while explicating their modes of action and health-beneficial impacts on aquatic animals with an exhaustive look at the available literature. A good grasp of the biological mechanisms assists principally in maximizing their beneficial properties and potential importance. Prospects and impediments are also discussed, along with implications for future investigations.

2. Disease threats in aquaculture

Though aquaculture is a promising path to ending global hunger and malnutrition, the industry is profoundly impacted by a range of communicable diseases that impose a substantial economic burden. The newly emerged coronavirus disease (COVID-19) has ushered in an unprecedented era of global pandemics of zoonotic origin and shifted our perspectives on farm animal diseases. Disease threats are by far the primary hindrance that impedes aquaculture production (Subasinghe et al., 2023). Most diseases, which commonly thrive under the conditions in commercial aquaculture settings (extensive, semi-intensive, and intensive production systems), are caused by primary or opportunistic (facultative) pathogens and can be broadly classified as bacterial, viral, fungal, or parasitic infections (Irshath et al., 2023; Jorgensen, 2020; Miccoli et al., 2021). The persistent occurrence of such diseases in aquaculture is typically accompanied by mass mortalities and production losses, which can have poor consequences for farmers, consumers, and the environment. The emergence and progression of disease can be the result of a series of interconnected events reflecting the interaction between the host, pathogens, and environment (Fig. 2) (MacKinnon et al., 2023). Stressful circumstances, including overcrowding, poor water conditions, and environmental deterioration, permit the transmission of the pathogen and the development of disease in the host (Lim

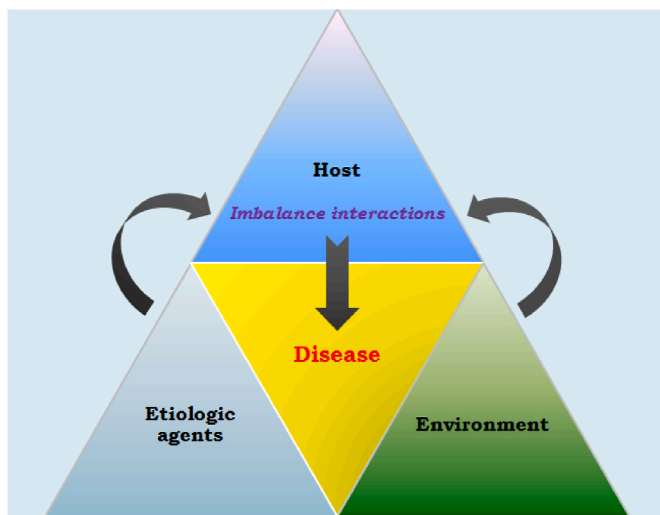


Fig. 2. Complex interactions between aquatic species, disease-causing agents, and the environment, where any disruption or imbalance in these interactions contribute to disease episodes.

et al., 2021). Nevertheless, diagnosis and assignment of aquatic disease causation can be inherently difficult, which is for the most part due to host complexity, the abundance of microorganisms, and the variable nature of aquatic habitats (Hutson et al., 2023). Timely diagnosis to confirm the etiology while enabling the response to diseases in aquatic ecosystems is a challenging but essential goal. Bacteria and viruses are accountable for most of the infectious diseases diagnosed in confined aquaculture, where they capitalize on a weakened or compromised host immune response, triggering serious complications (Flegel, 2019; Irshath et al., 2023). Compelling evidence from recent investigations pinpoints the serious impacts of emerging bacterial and viral diseases on worldwide aquaculture production (Abdelrahman et al., 2023; Algammal, Alfifi, et al., 2022; Combe et al., 2023; Elgendy et al., 2022; Kiat et al., 2023; Maldonado-Miranda et al., 2022; Wang, Kong, et al., 2021). Bacterial infections, specifically bacterial hemorrhagic septicemia, bacterial kidney disease (BKD), columnaris disease, edwardsiellosis (*Edwardsiella* septicemia), furunculosis, mycobacteriosis, streptococcosis, ulcerative disease, and vibriosis (*Vibrio* septicemia), amongst others, are prevalent and inflict substantial economic damages to the industry (Haenen et al., 2023; Irshath et al., 2023; Nachimuthu et al., 2021; Rowley, 2022). Massive mortalities were also documented in hatchery-reared aquatic animals linked to emerging viral diseases, such as infectious hematopoietic necrosis (IHN), heart and skeletal muscle inflammation (HSMI), tilapia lake virus (TLV) infection, infectious salmon anemia (ISA), viral hemorrhagic septicemia (VHS), viral covert mortality disease (VCMD), and white head disease (WHD), amongst others (Kibenge, 2019; Lee et al., 2022; Liao et al., 2022; Tavares et al., 2023; Valero & Cuesta, 2023). Lately, a range of other pathogens, including fungi (e.g., *Dermocystida destruens* and *Saprolegnia* spp.) (Gozlan & Combe, 2023; Meneses et al., 2023; Sarkar et al., 2022) and crustacean parasites (e.g., argulids, Rhizaria, and sacculinids) (Fazhan et al., 2020; Hunt et al., 2022; Merou et al., 2020), that pose significant risks to global aquatic biodiversity and aquaculture have also become the focus of considerable research. Extensive studies assessing the economic impacts associated with aquaculture diseases were previously published (Abdelrahman et al., 2023; Fernandez Sanchez et al., 2022; Nor et al., 2019; Patil et al., 2021; Peterman & Posadas, 2019; Yazid et al., 2021). Integrative reviews on infectious diseases in aquaculture have critically interpreted all aspects relevant to the molecular-based characterization of virulence and pathogenicity, AMR patterns and genes, as well as targeted preventive approaches (Abdelsalam et al., 2023; Algammal, Mabrok, et al., 2022; Samiappan et al., 2022;

Sanches-Fernandes et al., 2022; Talukder et al., 2021). Recent advances in molecular biology have nonetheless enormously extended our knowledge of these pathogens, particularly with respect to understanding virulence, pathogenicity, and complex host-pathogen interactions (Algammal, Mabrok, et al., 2022; Martinez et al., 2023; Sciuto et al., 2022). Therefore, with the advent of novel biologically-based technologies (e.g., biological control), aquaculture establishments must incorporate proactive disease management strategies and effective biosecurity to prevent disease outbreaks while fostering resilience in their production systems, which ultimately translates into the most profitable result and, thus, motivation for a sustainable industry.

3. The functional use of probiotics, prebiotics, synbiotics, paraprobiotics, and postbiotics

3.1. Probiotics and prebiotics

Intensive aquaculture practices have escalated the prevalence and severity of aquatic animal diseases. Animal husbandry is closely linked to health and welfare, and the gut microbiome is rapidly gaining recognition as a crucial determinant for production success. The gut microbiome is indispensable for animal health and assumes an integral role in an array of physiological processes, viz., growth performance, nutrient digestion and absorption, endogenous metabolism, production of enzymes, and immunity, amongst others (Diwan et al., 2022; Medina-Felix et al., 2023). Indisputably, the gut microbial community is, in turn, subject to alterations under the influence of many factors, including diet, developmental stages, diseases, stress, and environmental conditions (Chen et al., 2022; Hasan et al., 2023). A disrupted or altered gut microbiome typically corresponds to disease conditions and therefore serves as a valuable biological marker for stress exposure, metabolic potential, and health status (El-Saadony et al., 2022; Zhao et al., 2023). Therapeutic modulation strategies (i.e., the functional use of probiotics and prebiotics) have been implicated in the positive alteration or modulation of the gut microbiome (i.e., microbiota composition and diversity) of various aquatic species (Goh et al., 2023; Luna et al., 2022; Zhang, Lianslug, He, Feng, & Li, 2022).

The provision of probiotics as bioactive agents is a widely adopted and commercially accessible option for targeting the manipulation of the composition and function of the gut microbiome (Khanjani et al., 2024). Probiotics are non-pathogenic live microorganisms or microbial feed supplements that afford health benefits to the host when administered in satisfactory quantities (Hasan et al., 2023; Samat et al., 2020). Probiotics comprise numerous microorganisms, primarily bacteria, bacteriophages, yeast, fungi, and microalgae, which can be constantly or periodically incorporated, either alone or in combination, as feed supplements or water additives (Puvanasundram et al., 2021; del Valle et al., 2023). A good number of commercial mono- or multi-strain probiotics are presently available. Lactic acid bacteria (LAB) belonging to the genera *Bifidobacterium*, *Carnobacterium*, *Enterococcus*, *Lactobacillus*, *Lactococcus*, *Streptococcus*, and *Streptomyces* are the most extensively researched and well-characterized probiotics for use in aquaculture (Butt et al., 2024; Yilmaz et al., 2022; Yousuf et al., 2022). The effects of probiotic introduction are typically noticeable in the gut of animals. Evidently, the prominent effects of probiotics are principally reflected in bolstered growth performance and survival, improved gut microbiota and intestinal morphology, stimulated enzymatic secretion and activities, up-regulated gene expression, reinforced immune and antioxidant defense systems, and strengthened disease resistance, which likely derive from their gut modulatory properties (Zabidi et al., 2021; Assan et al., 2022; Sumon, Sumon, et al., 2022; Abdel-Latif et al., 2023a; Zhu, Kong, et al., 2023; Zhu, Wang, et al., 2023). Within this context, the plausible modes of action elucidated for probiotics in aquatic animal guts include, particularly: (i) secretion of antimicrobial or bioactive compounds (e.g., bacteriocins, defensins, hydrogen peroxide, lysozyme, and siderophores); (ii) anti-adhesive activity against pathogens; (iii)

competitive exclusion of pathogens; (iv) lowering of luminal pH; (v) fortification of intestinal barrier structure and function; and (vi) stimulation of local and systemic immune mechanisms, where the mechanistic details have been reiterated in previous discussions (El-Saadony et al., 2021; Kawser et al., 2022; Rohani et al., 2022; Sumon, Hussain, et al., 2022; Yilmaz et al., 2022). Similarly, the water-improving effect of probiotics indicated additional roles in reducing and preventing the accumulation of organic loads (e.g., nutrient recycling and the disintegration of organic matters) and the preservation of water quality that could otherwise lead to stress and toxicity in cultured animals (Bhakta et al., 2023; Kamilya & Devi, 2022; Zhang, Ji, et al., 2022). Notably, the wide spectrum of secreted inhibitory substances grants probiotics a competitive edge in outcompeting pathogenic strains while flourishing in the gut, water column, or substrate sediment (Sumon, Hussain, et al., 2022; Yilmaz et al., 2022). In actuality, the successful utilization of probiotics paved the way for a further concept, i.e., prebiotics. Prebiotics are classified as non-viable or selectively fermented food ingredients that stimulate the proliferation and activity of one or a limited number of beneficial indigenous gastrointestinal microbiota (Arun et al., 2023; Bondad-Reantaso et al., 2023; Goh et al., 2022). Some common prebiotics that have noteworthy aquaculture applications encompass arabinooligosaccharides (AXOS), fructooligosaccharides (FOS), galactooligosaccharides (GOS), inulin, isomaltooligosaccharides (IMO), mannooligosaccharides (MOS), and xylooligosaccharides (XOS) (Oviedo-Olvera et al., 2023; Wee et al., 2022). Previous investigations simultaneously identified an intimate link between prebiotic supplementation and growth promotion, enhanced immunity and antioxidant status, antimicrobial and disease resistance, as well as a promising alteration of the gut microbiota (Juarez et al., 2023; Panase et al., 2023; Xu et al., 2023; Zhou, Han, et al., 2023). Prebiotic metabolites (e.g., acetate, amino acids, butyrate, lactic acid, polyamines, and short-chain fatty acids), as fermented byproducts, contribute by functioning as a vital source of energy and growth inducer, sustaining the flourishing of beneficial bacteria, and maintaining the integrity of gastrointestinal epithelial cells, including mucus production, while antagonizing pathogen development (Bondad-Reantaso et al., 2023; Rohani et al., 2022; Vargas-Albores et al., 2021). Such modifications consequently result in specific changes in the gut morphology or barrier function as well as the composition and functional activity of the gastrointestinal microflora, which foster the health and well-being of the host (Rohani et al., 2022; Wang, Xu et al., 2022). Apart from that, these metabolites also exhibit potent antimicrobial, anti-inflammatory, antioxidant, and immunostimulatory properties (Goh et al., 2022; Mohan et al., 2022; Oviedo-Olvera et al., 2023). The advantageous attributes of probiotic microorganisms can be further improved through the combined use of prebiotics in a single treatment entity to unleash the greatest health benefits for farmed aquatic animals.

The use of probiotics and prebiotics serves as a safer alternative to antimicrobials for disease control, marking a new era in aquatic feed production. These approaches, when complemented with good husbandry practices, are particularly invaluable for maximizing aquatic production. Yet these therapies have their fair share of unresolved issues. The technologies or techniques for delivering probiotics or prebiotics must retain their viability and/or functionality, especially when used in aquatic settings. Research effort should also be put forth on emphasizing the impacts of treatment with multi-strain probiotics rather than mono-strains on distinct growth stages of various animals, taking into consideration that the favorable outcomes from most preliminary investigations are wholly species-specific and correspond to a single or specific development stage. Moreover, evaluating the efficacy of probiotics and prebiotics in commercial-scale setups holds significance, given that compelling research findings may not be producible on farm operations. Correspondingly, additional inquiry is warranted to identify the appropriate strain of probiotics or suitable prebiotic compounds, efficacious dosages, administration techniques, and the likelihood of AMR gene transfer from pathogens to probiotic microorganisms via

horizontal transference (Bondad-Reantaso et al., 2023; Daniali et al., 2020; Mawardi et al., 2023). Furthermore, much more information is necessitated for precisely establishing or explicating their exact mechanisms of action that pertain to the conferred health benefits while maintaining minimal ecological consequences through vigilant use. Following that, the therapeutic effects of probiotic and prebiotic products demand further analysis with next-generation molecular approaches paired with advancements in the omics field, given the intricacy of animal gut microbiota ecosystem dynamics. Nevertheless, the diverse therapeutic applications of probiotics and prebiotics represent a highly promising and environmentally friendly biological control strategy for preventive health care, supporting sustainability in aquaculture.

3.2. Synbiotics, paraprobiotics, and postbiotics

Synbiotics refer specifically to the conjunction between probiotics and prebiotics in a potent synergy that can optimize the beneficial effects of both (Yilmaz et al., 2022; del Valle et al., 2023). The prospective applications of synbiotics in aquaculture have sparked attention on account of all the additional health benefits beyond those observed for individual administration of either probiotics or prebiotics (Butt et al., 2021; Rohani et al., 2022; Shinde et al., 2023). The International Scientific Association for Probiotics and Prebiotics (ISAPP) consensus panel distinguished between two categories of synbiotics, i.e., complementary and synergistic (Swanson et al., 2020; Mounir et al., 2022; del Valle et al., 2023). A complementary type composed of a probiotic and a prebiotic, in which both act independently or non-cooperatively to benefit the host. The rationale behind well-designed synergistic synbiotics is that the prebiotics selectively stimulate the growth, metabolism, and persistence of the companion probiotics with minimal influence on other commensal microorganisms, thereby benefiting the host more advantageously. A wide range of probiotics (e.g., *B. coagulans*, *Bifidobacteria* spp., *Lactobacillus* spp., *Saccharomyces cerevisiae*, and *Saccharomyces boulardii*) and prebiotics (e.g., FOS, GOS, inulin, MOS, and XOS) have typically been incorporated into synbiotic formulations (Amenyogbe et al., 2020; Abdel-Latif et al., 2022; Alvanou et al., 2023; del Valle et al., 2023). Recent scientific attempts advocate the positive impacts of synbiotics on growth performance, hemato-biochemistry, gut microbiome, intestinal morphology, immunity, disease resistance, and physiological changes in a variety of aquatic species (Table 1). Nevertheless, systematic procedures and general criteria for developing synbiotics are apparently lacking in the field. Furthermore, the development and evaluation of synergistic synbiotics are formidably challenging and complicated. One cannot truly expect certainty that a random combination or pairing of a given probiotic with a specific prebiotic will bring about synergy. Rather, successful formulations of synbiotics require an appreciation of a substantial scientific basis on functional and metabolic aspects, as well as the ecological complexity of the gut environment as a whole (Goh et al., 2022; Quintero et al., 2022; Swanson et al., 2020). Undeniably, advancements in multiomics approaches and animal microbiome science continue to be significant for the development of efficacious synbiotics that deliver immense health benefits. As of late, the research focus has gradually diverted from using viable probiotic microorganisms to non-viable paraprobiotics (inactivated or dead probiotic cells) and postbiotics (reactive metabolic byproducts secreted by viable bacteria or discharged post-cell lysis) (Goh et al., 2022; Quintero et al., 2022; del Valle et al., 2023). Both elements are emerging concepts in aquaculture since they wield a broad range of health-promoting attributes on hosts, directly or indirectly, such as anti-inflammatory, antimicrobial, antioxidative, and immunostimulatory (Tables 2 and 3). Paraprobiotics can be derived by inactivating viable probiotics via ultraviolet treatment, ionizing radiation, ultrasonication, heat application, and formalin inactivation (Dominguez-Maqueda et al., 2021; Goh et al., 2022; Li & Tran, 2022). However, the inactivation process should be capable of retaining the

Table 1
Physiological and therapeutic relevance of synbiotics in aquaculture nutrition.

Animal species	Synbiotic mixture		Principal response	Reference
	Probiotic source	Prebiotic source		
Asian seabass (<i>Lates calcarifer</i>)	<i>Lactobacillus casei</i> (10 ⁹ CFU/mL) at 1 %	Garlic powder (<i>Allium sativum</i>) at 1 %	↑ mucosal immune responses and antioxidant status; improved intestinal morphology; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival to <i>Vibrio harveyi</i> infection	Siddik, Howieson, Islam, & Fotedar, 2022
Atlantic salmon (<i>Salmo salar</i>)	<i>Pediococcus acidilactici</i> (0.03 %)	FOS (0.1 %) and GOS (1 %)	↑ growth performance; improved gut health, endogenous metabolism, antioxidant status, and immune response	Dhanasiri et al. (2023)
Common carp (<i>Cyprinus carpio</i>)	<i>Bacillus licheniformis</i> (10 ⁷ CFU/g diet)	FOS (0.3 %)	↑ growth performance; ↑ digestive enzyme activities; improved hemato-biochemical indices and antioxidant status; ↑ plasma complement levels and lysozyme and acid phosphatase activities	Yuan et al. (2022)
	<i>Pediococcus acidilactici</i> at 1 g/kg diet (or 10 ¹⁰ CFU/kg diet)	IMO (5 and 10 g/kg diet)	↑ growth performance and feed utilization efficiency; improved hemato-biochemical indices and antioxidant status; ↑ serum complement levels and lysozyme activity; ↑ mucosal immune responses	Maniat et al. (2023)
	<i>Lactobacillus helveticus</i> (10 ⁷ and 10 ⁹ CFU/g diet)	Gum arabic (0.5 and 1 %)	↑ growth performance and feed utilization efficiency; ↑ digestive enzyme activities and intestinal microbiota; improved innate immune responses and antioxidant status; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Yousefi et al. (2023)
Fringed-lipped peninsular carp (<i>Labeo fimbriatus</i>)	<i>Bacillus subtilis</i> (10 ⁴ and 10 ⁶ CFU/g diet)	FOS (0.5 %)	↑ growth performance and feed utilization efficiency; ↑ digestive enzyme activities and intestinal morphology; improved hemato-biochemical indices; ↑ serum lysozyme and respiratory burst activities; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Pawar et al. (2023)
African catfish (<i>Clarias gariepinus</i>)	<i>Lactobacillus casei</i> (10 g/kg diet)	Hairy-fruited eggplant (<i>Solanum ferox</i>) (2, 4, and 6 g/kg diet)	↑ growth performance and feed utilization efficiency; improved immune responses; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> and <i>Pseudomonas fluorescens</i> infections	Hardi et al. (2022)
Hybrid catfish (<i>Clarias gariepinus</i> × <i>Clarias macrocephalus</i>)	<i>Acinetobacter</i> KU011TH (10 ⁸ , 10 ⁹ , and 10 ¹⁰ kg ⁻¹ diet)	Chitosan (coated at 20 mL/kg diet)	improved hematological indices and serum immune parameters; ↑ mRNA expression levels of immune-related genes in the head kidney, liver, and spleen; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Say et al. (2023)
Nile tilapia (<i>Oreochromis niloticus</i>)	<i>Pediococcus acidilactici</i> (0.2 %)	Pistachio hull polysaccharide (0.1 %)	↑ growth performance; ↑ serum alternative complement, lysozyme, and alkaline phosphatase activities; improved serum biochemistry and antioxidant status; ↑ digestive enzyme activities; ↑ skin mucosal immunity; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Mohammadi et al. (2022)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	<i>Pediococcus acidilactici</i> (10 ⁶ CFU/g diet)	GOS (1 %)	↓ salmonid-related Candidatus Mycoplasma salmoninae in the gut; improved gut microbiota and health	Rasmussen et al. (2022)
Sobaity seabream (<i>Sparidentex hasta</i>)	<i>Lactobacillus plantarum</i> (10 ⁶ CFU/g diet)	XOS (5 and 10 g/kg diet)	↑ digestive enzyme activities; ↑ mRNA expression levels of growth- and immune-related genes	Agh et al. (2022)
European crayfish (<i>Astacus astacus</i>)	<i>Lactobacillus reuteri</i> (5 × 10 ⁶ CFU/g diet) and <i>Bacillus clausii</i> (5 × 10 ⁶ CFU/g diet)	Polyphenols from olive leaf extract (0.25 mg/g diet)	↑ growth performance, body condition, and survival; improved gastrointestinal microbiota	Sateriale et al. (2023)
Narrow-clawed crayfish (<i>Pontastacus leptodactylus</i>)	<i>Lactobacillus plantarum</i> (10 ⁷ , 10 ⁸ , and 10 ⁹ CFU/g diet)	GOS (1 %)	improved hemato-biochemical indices; ↑ digestive enzyme activities; enhanced immune responses, intestinal microbiota, antioxidant status, and stress resistance	Nedaei et al. (2023)
Chinese Mitten Crab, (<i>Eriocheir sinensis</i>)	Multi-strain probiotics (each gram contains <i>Lactobacillus acidophilus</i> 10 ⁶ CFU, <i>Bacillus subtilis</i> 10 ⁷ CFU, and <i>Saccharomyces cerevisiae</i> 10 ¹⁰ CFU) at 2 g/kg diet	FOS (5 g/kg diet)	↑ growth performance and feed utilization efficiency; improved hepatopancreas protection; ↑ catalase and superoxide dismutase activities;	Wan et al. (2022)

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Table 1 (continued)

Animal species	Synbiotic mixture		Principal response	Reference
	Probiotic source	Prebiotic source		
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	<i>Bacillus subtilis</i> (1.0×10^{10} CFU) and <i>Saccharomyces cerevisiae</i> yeast (1.2×10^{11} CFU) from a commercial synbiotic at 3 g/kg diet	β -glucan, MOS, and <i>Bacillus subtilis</i> fermentation and yucca extracts from a commercial synbiotic at 3 g/kg diet	↓ malondialdehyde activity; ↑ antioxidant status and tolerance to transport stress ↑ growth performance and feed utilization efficiency; improved activities of acid phosphatase, alkaline phosphatase, catalase, lysozyme, and total superoxide dismutase in hemolymph; enhanced intestinal morphology and microbiota; ↑ innate immune responses, disease resistance, and survival to <i>Vibrio parahaemolyticus</i> infection	Yao et al. (2021)
	<i>Pediococcus pentosaceus</i> (10^6 , 10^7 , and 10^8 kg ⁻¹ diet)	FOS (0.5 %)	↑ growth performance; improved hemocyte count as well as phenoloxidase and lysozyme activities; ↑ immune response and disease resistance against <i>Vibrio parahaemolyticus</i>	Hong et al. (2022)
	<i>Bacillus amyloliquefaciens</i> , <i>Bacillus pumilus</i> , and <i>Bacillus subtilis</i> (mixed in pairs at a ratio of 5×10^8 : 5×10^8 CFU/kg diet)	Chitosan (coated at 20 mL/kg diet)	↑ growth performance and feed utilization efficiency; ↑ mRNA expression levels of growth- and immune-related genes; improved hepatopancreas features as well as epithelial and intestinal wall thicknesses; ↑ immune response and disease resistance against AHPND caused by <i>Vibrio parahaemolyticus</i>	Kewcharoen and Srisapoome (2022)
	<i>Leuconostoc mesenterioide</i> B4 (10^7 CFU/g diet)	Dextran (0.05 %)	↑ growth performance and feed utilization efficiency; enhanced hematological indices; improved intestinal morphology and microbiota; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival to <i>Vibrio parahaemolyticus</i> infection	Huang et al. (2023)

Abbreviations: AHPND, Acute hepatopancreatic necrosis disease; FOS, fructooligosaccharide; GOS, galactooligosaccharides; IMO, isomaltooligosaccharide; mRNA, messenger ribonucleic acid; MOS, mannan oligosaccharide; XOS, xylooligosaccharide.

beneficial properties of the probiotic microorganisms. Contrarily, the many postbiotic molecules comprise primarily bacteriocins, secreted biosurfactants, fatty acids, flavonoids, polysaccharides, teichoic acids, transmembrane proteins, and terpenoids, amongst others (Ang et al., 2020; Sudhakaran et al., 2022). The concerns surrounding the use of probiotics spurred interest in the adoption of paraprobiotics and postbiotics, which were previously entirely uncommon. The latter imparts multiple features that prevail over live microorganisms, viz.: (i) easy preparation and storage; (ii) availability in purest forms with identified molecular structures; (iii) safety of use; and (iv) specific mechanisms of action with superior functionality (Mehta et al., 2023; Monteiro et al., 2023; Nataraj et al., 2020; Rafique et al., 2023). When non-viable cells are used, the odds of horizontal transference of AMR genes are bound to be the lowest. There is presently inadequate information for an exhaustive understanding of the intricate effects of paraprobiotics and postbiotics and their specific mechanistic actions on the animal gut microbiome that pertains to aquatic species (Abdel-Latif et al., 2022; Goh et al., 2022). Further research remains necessary to decipher the extensive modes of action, define the optimal dose and route of administration, improve production methods and product stability, and establish strategies for product quality control that may uncover novel uses in aquaculture. Collectively, the utilization of synbiotics, paraprobiotics, and postbiotics, as a step beyond probiotics and prebiotics, constitutes a profoundly promising and acceptable proposition in aquatic disease management and is anticipated to become more widely employed in the future.

4. The role of phytochemicals

Phytochemicals, or phytobiotics, are plant-derived (botanical) feed

ingredients or additives containing a cocktail of biologically active principles (e.g., alkaloids, glycosides, flavonoids, polypeptides, polyphenols, saponins, and terpenoids) utilized in animal nutrition (Ibrahim et al., 2022; Kesselring, Gruber, Standen, & Wein, 2021; Valente et al., 2021). Feed phytochemicals may be broadly categorized based on their botanical origins or parts of the plant (e.g., herbs and spices), processing methods (e.g., essential oils and oleoresins), and chemical composition (which varies depending on sources and geographical regions, climatic conditions, harvest time, processing techniques, and storage conditions) (Kesselring, Gruber, Standen, & Wein, 2021; Pandey et al., 2019). These plant materials are usually non-toxic and relatively safe for humans, animals, and the environment. Botanicals or phytochemical extracts were authorized for use as sensory additives or flavoring compounds that fall within the scope of European legislation (Caipang, 2020; Wang, Su, et al., 2021). Phytochemicals exert a broad spectrum of distinct biological activities, including anti-inflammatory, anti-microbial, antioxidative, anti-stress, and immunostimulatory, amongst others, which are well-defined and supported by available scientific evidence (Ali et al., 2022; Liao et al., 2022; Mohammady et al., 2022; Sinha et al., 2021; Zhu, 2020). The distinctive flavor attributes (aromatic) of phytochemicals are reputed to have positive impacts on feed palatability (Burducea et al., 2022; Zaminhan-Hassemer et al., 2022). Their usage is renowned as beneficial for the growth and development, health, and welfare of farmed animals, thus rendering physiological benefits beyond conventional feeding practices. Phytochemical administration is seemingly a way forward to curb infectious diseases in aquaculture.

Research on phytochemicals as functional components in various aspects of aquatic animal production has accelerated rapidly in recent times. Scientific reports on the immunostimulatory effects and therapeutic benefits of phytochemicals in aquatic species, through both *in vitro* and *in*

Table 2
Physiological and therapeutic relevance of paraprobiotics in aquaculture nutrition.

Animal species	Paraprobiotic source and inactivation method	Inclusion level	Principal response	Reference
Atlantic salmon (<i>Salmo salar</i>)	<i>Lactiplantibacillus plantarum</i> strain L-137; heat inactivation	20, 100, and 500 mg/kg diet	enhanced physiological and immune responses; improved intestinal microbiota; ↑ tolerance to stressful conditions	Rocha et al. (2023)
Common carp (<i>Cyprinus carpio</i>)	<i>Lactiplantibacillus plantarum</i> ; heat inactivation	50 and 100 mg/kg diet	↑ growth performance; improved intestinal morphology; ↑ mRNA expression levels of antioxidant and immune-related genes; ↑ tolerance to thermal stress	Yassine et al. (2021)
	<i>Saccharomyces cerevisiae</i> (1×10^{10} cells/g), <i>Bacillus velezensis</i> (2×10^{10} cells/g), and <i>Cetobacterium somerae</i> (5×10^8 cells/g); heat inactivation	1, 2, and 3 g/kg diet	↓ hepatic lipid deposition; ↓ intestinal and liver damage and inflammation; enhanced innate immune responses and antioxidant status; improved gut microbiota;	Meng et al. (2023)
Gilthead seabream (<i>Sparus aurata</i>)	<i>Saccharomyces cerevisiae</i> from a commercial source; heat inactivation	5 %	improved intestinal microbiota by promoting the proliferation of beneficial bacteria	Rimoldi et al. (2020)
Hybrid sturgeon (<i>Acipenser baerii</i> x <i>Acipenser schrenckii</i>)	<i>Rhodotorula minuta</i> and <i>Cetobacterium somerae</i> from a commercial source; heat inactivation	5 g/kg diet	↑ growth performance; ↑ composition of the gut microbiota; ↑ mRNA expression levels of growth-, anti-inflammatory-, and immune-related genes	Wu et al. (2020)
Indian major carp (<i>Catla catla</i>)	<i>Bacillus amyloliquefaciens</i> FPTB16; heat inactivation	10^7 , 10^8 , and 10^9 CFU/g diet	↑ serum lysozyme activity and total protein content; ↑ myeloperoxidase and alkaline phosphatase activities; ↑ mRNA expression levels of immune-related genes in the liver and head kidney	Singh et al. (2017)
Largemouth bass (<i>Micropterus salmoides</i>)	<i>S. cerevisiae</i> and <i>Cyberlindnera jadinii</i> from a commercial source; heat inactivation	800 mg/kg diet	↑ growth performance; ↑ intestinal permeability and peptide transport; improved gut microbiota and health;	Xie et al. (2022)
Largemouth bass (<i>Micropterus salmoides</i>)	<i>S. cerevisiae</i> and <i>Cyberlindnera jadinii</i> from a commercial source; heat inactivation	800 mg/kg diet	↓ hepatic lipid deposition and total plasma bile acid content; improved gut microbiota and liver health	Xie et al. (2023)
Striped catfish (<i>Pangasionodon hypophthalmus</i>)	<i>Bacillus subtilis</i> ; heat inactivation	0.5, 1, and 2 g/kg diet	↑ growth performance and feed utilization efficiency; improved intestinal morphology; ↑ digestive enzyme activities; enhanced innate immune responses and antioxidant status	Shawky et al. (2023)
Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	<i>Lactiplantibacillus plantarum</i> ; heat inactivation	10^7 , 10^8 , and 10^9 CFU/g diet	enhanced innate immune responses; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Dash et al. (2015)
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	<i>Lactiplantibacillus plantarum</i> ; heat inactivation	Coating with <i>Lactiplantibacillus plantarum</i> preparation (0.01 mL/g diet)	↑ composition of the gut microbiota; improved gut health	Zheng et al. (2020)
	<i>Clostridium butyricum</i> CBG01; heat inactivation	1×10^{11} CFU/kg feed	↑ growth performance and feed utilization efficiency; enhanced humoral immune responses and antioxidant status; ↑ mRNA expression levels of growth-, antioxidant-, and immune-related genes; ↑ disease resistance and survival to <i>Vibrio parahaemolyticus</i> infection	Luo et al. (2021)
	<i>Pediococcus pentosaceus</i> PP4012; heat inactivation	10^5 and 10^6 CFU/g diet	↑ growth performance, feed utilization efficiency, and survival; enhanced innate immune responses; ↑ composition of the gut microbiota and health; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival to <i>Vibrio parahaemolyticus</i> infection	Ballantyne et al. (2023)

Abbreviations: mRNA, messenger ribonucleic acid.

in vivo assessments, are accessible (Table 4). The application of functional diets incorporating substances of plant origin has been demonstrated to be an effective tool that induces reinforcement or modulation of animal immunity, stress tolerance (abiotic and biotic), and disease resistance as part of a proactive strategy to manage aquatic animal health and diseases while improving production performance (Firmino, Galindo-Villegas, Reyes-Lopez, & Gisbert, 2021; Hossain et al., 2023; Ibrahim et al., 2022). Interestingly, the protective effects of phytochemicals, which may be, for the most part, credited to their

anti-inflammatory and anti-oxidative properties, were elucidated for a range of phytochemical active ingredients, with progress in the identification and mechanistic studies of these components in various aquatic animals (Beltran & Esteban, 2022; Liu, Zhu, et al., 2022; Mohammady et al., 2022; Serradell et al., 2023). Apart from that, concerning growth performance, animals substantially profit from enhancements in digestibility, the function of gastrointestinal or gut microbiota, intestinal morphology, and nutrient assimilation, which consequently translate into a higher level of performance (Liu, Zhu, et al., 2022; Moghadam

Table 3
Physiological and therapeutic relevance of postbiotics in aquaculture nutrition.

Animal species	Postbiotic source	Inclusion level	Principal response	Reference
Common carp (<i>Cyprinus carpio</i>)	Cell-free supernatants of <i>Cetobacterium somerae</i> and <i>Lactococcus lactis</i> (10^9 mL ⁻¹ each) in dry form	0.2 and 0.3 g/kg diet	improved intestinal microbiota and morphology; promoted liver and gut health; ↑ mRNA expression levels of antioxidant, anti-inflammatory-, and immune-related genes; enhanced mucosal immunity, antioxidant status, and anti-inflammatory response	Yu et al. (2023)
European seabass (<i>Dicentrarchus labrax</i>)	Cell-free sonicated extract of <i>Shewanella putrefaciens</i> Pdp11	6.3 µg total amount of proteins/g diet	↑ immune response involved in antiviral activity; ↓ replication of the nervous necrosis virus; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival against the nervous necrosis virus	Moreno et al. (2023)
Hybrid sturgeon (<i>Acipenser baerii</i> x <i>Acipenser schrenckii</i>)	Metabolic components of <i>Rhodotorula minuta</i> and <i>Cetobacterium somerae</i> from a commercial source	5 g/kg diet	↑ growth performance; ↑ composition of the gut microbiota; ↑ mRNA expression levels of growth-, anti-inflammatory-, and immune-related genes	Wu et al. (2020)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	Micronized <i>Lactobacillus</i> fermented feed product (containing alfalfa and soy flours)	3 mg/g diet	↑ composition, diversity, and richness of the gut microbiota; ↑ disease resistance and survival against <i>Lactococcus garvieae</i> infection	Mora-Sanchez et al. (2020)
	Micronized fermented feed product (containing alfalfa and soy flours) containing lactic acid bacteria	3 mg/g diet	↑ composition, diversity, and richness of the gut microbiota; ↑ disease resistance and survival against <i>Lactococcus garvieae</i> infection	Perez-Sanchez et al. (2020)
	Micronized fermented feed product (containing alfalfa and soy flours) containing lactic acid bacteria from the genus <i>Lactobacillus</i> and <i>Leuconostoc</i>	3 mg/g diet	↑ mRNA expression levels of immune-related genes	Perez-Sanchez, Mora-Sanchez, Jiron, Flores, & Balcazar, 2021
Bullfrog (<i>Lithobates catesbeiana</i>)	Cell-free extract and supernatant of <i>Bacillus subtilis</i> LCBS1 (8×10^7 CFU/mL)	Coating with <i>Bacillus subtilis</i> preparation (1 mL/g diet)	↑ growth performance and feed utilization efficiency; ameliorate enteritis; improved immune responses, antioxidant status, and intestinal health	Tao et al. (2023)
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	Fermented supernatant and cell-free sonicated extract of <i>Clostridium butyricum</i>	120 mL/kg diet (fermented supernatant); 1×10^{11} CFU/kg diet (cell-free extract)	↑ growth performance; improved intestinal morphology; ↑ mRNA expression levels of immune-related genes; ↑ disease resistance and survival against <i>Vibrio parahaemolyticus</i> infection	Li et al. (2019)
	Fermented supernatant and cell-free sonicated extract of <i>Lactiplantibacillus plantarum</i>	Coating with <i>Lactiplantibacillus plantarum</i> preparation (0.01 mL/g diet)	↑ composition of the gut microbiota; improved gut health	Zheng et al. (2020)
	Cell-free extract and supernatant of <i>Bacillus licheniformis</i> BCR 4-3 and <i>Vibrio parahaemolyticus</i> IPNGS16 in dry form	Both at 1 g/kg feed	improved intestinal microbiota; ↑ mRNA expression levels of superoxide dismutase, crustin, and penaeidin4; ↑ antimicrobial activity; ↑ immunity and survival	Vega-Carranza et al. (2023)

Abbreviations: mRNA, messenger ribonucleic acid.

et al., 2023; Zaminhan-Hassemer et al., 2022). The abovementioned factors are directly interrelated and crucial for animals' growth potential, health, and well-being. Some phytochemicals and their primary components have also exhibited the QSI mechanism to subdue deleterious microbial infections (Ibrahim et al., 2022; Rahimi et al., 2022; Reddy et al., 2022; Salomon et al., 2022). More recently, the exquisite art of formulating phytochemical-based diets corresponds to a suitable combination of plant materials that work harmoniously or synergistically together, often with superior potencies, and this necessitates a comprehensive grasp of their mechanistic and biological properties (Burducea et al., 2022; Goh et al., 2023; Serradell et al., 2023). Undoubtedly, the findings of such investigations have been mostly inconsistent, and the mechanisms or regulatory properties remain inconclusive with inadequate understanding and resources. This, however, ought to be explored more thoroughly under standardized conditions. Commercial phytochemical additives, for instance, feature typical blends of assorted botanical extracts with a mixture of active principles, which would make a systematic assessment of their potential efficacy challenging. It is within our expectation that significant contributions

from molecular genomic research and the integration of multi-omics strategies should favorably assist in further comprehending the mechanisms underlying the modes of action of phytochemicals, thereby facilitating the development of viable and cost-effective methods of employing them in aquatic animal feed. Apart from that, it should be emphasized that contemporary approaches and dedicated methodologies are required to precisely define or establish the effective concentration and route of administration of different phytochemicals. The deployment of cutting-edge technologies, mainly the emulsion and encapsulation of active ingredients, undeniably affords great avenues to optimize the pharmacokinetics and functionality of phytochemical feed additives (Abdel-Tawwab et al., 2022; Alagawany et al., 2021; Firmino, Galindo-Villegas, Reyes-Lopez, & Gisbert, 2021; Hashem et al., 2023). In this sense, functional feeds based on phytochemicals represent an efficacious, sustainable, and potentially safe prophylactic strategy for aquaculture with multiple benefits.

Table 4
Physiological and therapeutic relevance of phytogetic feed additives in aquaculture nutrition.

Animal species	Phytogetic source	Inclusion level	Principal response	Reference
Asian seabass (<i>Lates calcarifer</i>)	Liquorice (<i>Glycyrrhiza uralensis</i>) powder	1 %, 3 %, and 5 %	↑ growth and survival; ↑ mRNA expression levels of immune-related genes in fish liver and kidney	Yang et al. (2020)
	Fermented lemon (<i>Citrus limon</i>) peel	1 %, 3 %, and 5 %	↑ immune response and intestinal health; ↑ lysozyme activity	Zhuo et al. (2021)
Atlantic salmon (<i>Salmo salar</i>)	A commercial PFA (NatControl®) containing labdane diterpenes from green chiretta (<i>Andrographis</i> sp.)	0.5 g/kg diet	↑ mRNA expression levels of immune-related genes (<i>IL-12</i> and <i>IFN-1 genes</i>); ↑ cellular protection of SHK-1 cells; ↑ disease resistance and survival to <i>Piscirickettsia salmonis</i> infection	Romero et al. (2021)
	Leaf extracts from sage (<i>Salvia officinalis</i>) and lemon verbena (<i>Lippia citriodora</i>)	0.1 %	↑ somatic growth; ↑ systemic immune response; ↑ disease resistance and survival to <i>Aeromonas salmonicida</i> infection	Salomon et al. (2022)
European seabass (<i>Dicentrarchus labrax</i>)	A mixture of garlic and Labiatae essential oil	0.02 %	↑ stress tolerance and protection of head kidney leucocytes from apoptosis; ↑ lysozyme activity	Serradell et al. (2020)
Gilthead seabream (<i>Sparus aurata</i>)	A microencapsulated PFA containing synthetic garlic essential oil, carvacrol, and thymol	0.5 %	↑ mucosal immune responses and the secretion of non-specific immune molecules into the skin mucus; ↑ recruitment of phagocytic cells; ↓ oxidative stress and the capacity of bacterial proliferation in skin mucus	Firmino, Fernandez-Alacid, et al. (2021)
Great sturgeon (<i>Huso huso</i>)	Rosemary (<i>Rosmarinus officinalis</i>) essential oil	0.01 %, 0.1 %, 1 %, and 2 %	↑ hematological indices and immune response	Ebrahimi et al. (2020)
Common carp (<i>Cyprinus carpio</i>)	Cornelian cherry (<i>Cornus mas</i>) fruit extract	0.25 %, 0.5 %, and 1 %	↑ growth performance; ↑ lysozyme activity and serum total immunoglobulin; ↑ mRNA expression levels of antioxidant and immune-related genes; ↑ disease resistance and survival to <i>Aeromonas hydrophila</i> infection	Ahmadifar et al. (2022)
Common carp (<i>Cyprinus carpio</i>)	A blend of herbal extracts from marjoram (<i>Origanum majorana</i>), thyme (<i>Thymus vulgaris</i>), and summer savory (<i>Satureja hortensis</i>)	0.5 %, 1 %, 2 %, and 3 %	↑ feed utilization efficiency and growth performance; ↑ mucosal immune responses and antioxidant status	Rudiansyah et al. (2022)
Nile tilapia (<i>Oreochromis niloticus</i>)	Curcumin (from turmeric, <i>Curcumin longa</i>) nanoparticles	15, 30, 45, and 60 mg/kg diet	↑ growth performance; improved hemato-biochemical indices and intestinal morphology; ↑ digestive enzyme activities; ↑ antioxidant status and humoral immune response	Abdel-Tawwab et al. (2022)
	Thymol and thymoquinone as phenolic compounds from thyme (<i>Thymus vulgaris</i>) and black cumin (<i>Nigella sativa</i>) essential oils	Either singly (200 mg/kg diet) or in combination (1:1 ratio; 200 mg/kg diet)	↑ growth performance; ↑ expression levels of multiple genes encoding digestive and antioxidant enzymes; ↑ inflammatory responses; ↑ humoral immune responses and disease resistance against <i>Aeromonas sobria</i> ; ↓ expression of virulence genes in <i>Aeromonas sobria</i>	Ibrahim et al. (2022)
Rohu (<i>Labeo rohita</i>)	Ginger (<i>Zingiber officinale</i>) powder	5, 10, 15, and 20 g/kg diet	↑ growth performance; ↑ activities of liver enzymes; improved hemato-biochemical indices and antioxidant status	Rawat et al. (2022)
Striped catfish (<i>Pangasionodon hypophthalmus</i>)	Milk thistle extract (<i>Silybum marianum</i>)	0.1 %, 0.2 %, and 0.3 %	↑ growth performance; ↑ digestive enzyme activities; improved liver function and intestinal morphology; ↑ lysozyme activity and serum total immunoglobulin; ↑ antioxidant status and immune response	Abdel-Latif et al. (2023b)
Caspian roach (<i>Rutilus caspicus</i>)	Summer savory (<i>Satureja hortensis</i>) essential oil	100, 200, and 400 mg/kg diet	↑ growth performance and survival; improved hemato-biochemical indices and antioxidant status; ↑ tolerance to salinity stress; ↑ mucosal and humoral immune responses	Ghafariarsani et al. (2022)

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Table 4 (continued)

Animal species	Phytogenic source	Inclusion level	Principal response	Reference
Giant tiger prawn (<i>Penaeus monodon</i>)	Cannonball mangrove (<i>Xylocarpus granatum</i>) leaf extract	0.75, 1, and 1.25 × 10 ⁻⁶ (immersion bath therapy)	↑ total hemocyte count and phagocytic activity; ↑ survival rate and disease resistance against <i>Vibrio harveyi</i> infection; ↑ recuperative ability; ↓ virulence of <i>Vibrio harveyi</i>	Saptiani et al. (2020)
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	A commercial phytogenic feed additive containing Indian gooseberry (<i>Emblica officinalis</i>), ashwagandha (<i>Withania somnifera</i>), and holy basil (<i>Ocimum sanctum</i>)	0.5 and 1 g/kg diet	↑ tolerance to salinity stress; ↑ survival rate and disease resistance against the white spot syndrome virus	Selvam et al. (2020)
	A matrix-encapsulated phytogenic additive containing citrus, oregano (<i>Origanum vulgare</i>), and thyme (<i>Thymus vulgaris</i>) essential oils	200 and 400 mg/kg diet	↑ growth performance and survival; ↑ total hemocyte count and respiratory burst activity; improved health status	Kesselring, Gruber, Standen, & Wein, 2021
	Turmeric (<i>Curcumin longa</i>), curcumin, and curcumin nanomicelles	Turmeric (2.5–10 g/kg diet); curcumin (75–300 mg/kg diet)	↑ growth performance and survival; ↑ antioxidant status and immune response	Moghadam et al. (2021)

Abbreviations: IFN-1, type-1 interferon; IL-12, interleukin-12; mRNA, messenger ribonucleic acid; PFA, phytogenic feed additive; SHK-1, salmon head kidney cell line.

5. Exploiting quorum-sensing interference (QSI)

Quorum sensing (QS), or quorum signaling, is a definitive mechanism belonging to the complex bacterial communication system that enables specific processes to be governed or regulated, including virulence factor expression, biofilm formation, bioluminescence, stress adaptation, motility, secretion of secondary metabolites, horizontal gene transfer, and the regulation of gene expression accordingly, mediated by autoinducers (AIs) (diffusible chemical signal molecules) (Defoirdt, 2023; Mauritzen et al., 2023; Zhu, Chen, et al., 2023). A diversity of AIs was extensively reported to induce QS, such as auto-inducing peptides (AIPs), acyl-homoserine lactones (AHLs), epinephrine, norepinephrine, indole, ketones, and fatty acids, amongst others. The manipulation of microbial QS has piqued interest across several industries (e.g., agriculture, aquaculture, food, pharmaceuticals, and waste treatment), as it unlocks novel avenues for an array of therapeutic and industrial applications (Abbamondi & Tommonaro, 2022; Naga et al., 2023; Zhu, Chen, et al., 2023).

Noteworthy, stemming from the discovery of such a mechanism, many enzymes and chemical compounds (QS inhibitors) of diverse origins that interfere with or repress QS, with differing degrees of potency, have been identified and characterized (Defoirdt, 2023; Muller et al., 2023; Sun et al., 2022). When the QS systems are disturbed, microbial cells lose their pathogenicity and thus the tendency to cause diseases. The inhibition of QS, dubbed quorum-sensing interference (QSI), or quorum-quenching, has become an impetus for exploring novel practical approaches to control and mitigate bacterial infections in aquaculture systems. The aforementioned presents a compelling opportunity to suppress undesirable bacterial exhibits regulated through signaling, particularly biofilm formation and pathogenicity correlated with infectious diseases. Aside from infection control, QSI has also been the focal point of modern microbiological studies, with implications for host-pathogen interactions as well as microbial physiology and ecology (Escobar-Mucino et al., 2022; Rehman et al., 2022). The disruption of bacterial QS is achievable via several means, including but not limited to: (i) inhibition or interference of AI synthesis through the blockage of AI-2 synthase or receptor complex; (ii) extracellular hydrolysis or degradation of AIs by QSI enzymes, such as acylases, AHL-lactonase, and oxidoreductase; or (iii) scavenging of AIs by QSI antibodies and macromolecules (e.g., cyclodextrins) (Escobar-Mucino et al., 2022; Remy et al., 2018; Sikdar & Elias, 2020). Nevertheless, the efficacy of the above QSI strategies is subject to further extensive *in vivo* experimentation in host models for the management of aquaculture diseases. In fact, many compounds derived from algae, bacteria, and plants mimic the QS signals of bacteria, which in turn interfere with bacterial QS mechanisms and their regulated activities, as evidenced by prior

research (Alexpandi et al., 2021; Dow, 2021; Mishra & Muthukaliannan, 2022; Pande et al., 2015; Vikram et al., 2011; Zhu, Chen, et al., 2023). In recent years, the biochemical attributes of QSI enzymes have been rigorously evaluated, including their stability, kinetic properties, and capacity to inhibit microbes *in vivo* and *in vitro* for therapeutic applications in aquatic animal health (Rehman et al., 2022; Reina et al., 2022; Zhu, Chen, et al., 2023). A range of QSI enzymes with variable substrate specificity, stability, affinity, and catalytic efficiency under varying environmental circumstances is crucial for effective utilization and expanded application potential (Billot et al., 2020; Rehman et al., 2022; Remy et al., 2020). Additionally, numerous *Bacillus* species can act as quorum-quenching bacteria capable of extracellularly degrading AHLs, which are accountable for the expression of virulence factors in aquatic Gram-negative bacterial pathogens mediated by QS, with reference to specific recent reports (Chen et al., 2020; James et al., 2021; Santos et al., 2021; Shaheer et al., 2021). A novel approach was adopted lately to investigate the quorum quenching capacity of some halophilic marine bacilli strains isolated from coral mucus to combat *Vibrio parahaemolyticus*, a causative agent of early mortality syndrome (EMS) in shrimp aquaculture, and the results were startlingly promising (Muller et al., 2023). Notably, the bacilli strains were able to disrupt the QS molecules of *V. parahaemolyticus in vitro* and deter it from achieving the threshold for pathogenicity activation, which perhaps offers a long-term solution to EMS. Zhang, Yang, Eggermont, & Defoirdt, 2023 recently put forth a comprehensive discussion on the many inhibitory agents (both natural and synthetic) that hinder the QS systems in pathogenic vibrios, corresponding to the Harveyi and Splendidus clades, which potentially safeguard aquatic species from vibriosis. Moreover, advancements in next-generation sequencing methods or technologies and molecular genomics effectively enable researchers to gain mechanistic insights into the strength and nature of these interactions (Lin et al., 2022; Muthukrishnan et al., 2022; Yusof et al., 2022; Zhang et al., 2023). Despite QSI seeming to be a doable approach for reducing pathogenicity, it is not uncommon that bacterial agents may evolve resistance against various QS inhibitors as readily as they do to antimicrobials (Borges & Simoes, 2019; Helmy et al., 2023; Patel et al., 2023). Even so, it has been argued that the likelihood of bacteria building resistance to QS inhibitors is somewhat lower than that of conventional antimicrobial therapy (Patel et al., 2023; Salman et al., 2023; Zhang, Yang, Eggermont, & Defoirdt, 2023). It is generally acknowledged that QSI would pose minimal or no direct selective pressure on bacteria. Aspects of microbial resistance to QSI have been meticulously reviewed previously (Kalia et al., 2014; Krzyzek, 2019; Liu et al., 2018; Patel et al., 2023). The potential of bacteria acquiring resistance to QS inhibitors is prompting an entirely new line of research to explore substitutive QSI-based therapeutic strategies (e.g., using probiotics and macro- or microalgae) to

prevail over microbial QSI resistance (Davares et al., 2022; Natrah et al., 2022; Nurarina et al., 2020; Salman et al., 2023). Additional research is imperative to establish the magnitude to which external environmental factors and competition amongst individuals of the complex microbial community may influence the mechanisms of QSI. Nonetheless, QSI is featured among the most promising preventative measures for the environmentally sound management of rapidly emerging aquaculture diseases.

6. Phage therapy as a renewed approach

The phage approach, which involves the use of bacteriophage or bacteria-specific viruses, was first implemented in the early 20th century (around 1919) as a promising therapy to treat bacterial infections (Kowalska et al., 2020; Strathdee et al., 2023). This practice, however, struggled to develop, and its momentum was rapidly diminished by the successful introduction of antibiotics. Now, with the increasing prevalence of AMR, the spotlight is shining once again on phage therapy, rekindling interest in its use to precisely control undesired bacterial pathogens in a more environmentally sustainable way (Fabijan et al., 2023; Pereira et al., 2022). Phages (or bacteriophages) are ubiquitous viruses capable of specifically infecting and exterminating bacterial cells that carry their unique complementary receptors (specific host range) (Costa et al., 2022; Elois et al., 2023). Intriguingly, phages, as non-living biological entities, are inherently non-toxic or harmless to humans, animals, plants, and the environment, as they comprise primarily nucleic acids and proteins (Endersen & Coffey, 2020; Zia & Alkheraije, 2023). Phages are, therefore, considered safe and well tolerated by animal and plant cells, given that they replicate solely in the target bacterium. Much progress has been made on the potential application of phage therapy in agriculture (Ahmed & Li, 2023; Farooq et al., 2022; Oueslati et al., 2022), aquaculture (Liu, Han, et al., 2022; Ramos-Vivas et al., 2021), food safety (Imran et al., 2023; Islam et al., 2022; Lavilla et al., 2023; Wagh et al., 2023), wastewater treatment (Bolsan et al., 2022; Pallavali et al., 2023; Runa et al., 2021), and human and veterinary medicine (Costa et al., 2022; Fabijan et al., 2023; Ferriol-Gonzalez & Domingo-Calap, 2021; Grabowski et al., 2022).

Phages have been incorporated into therapy for aquaculture diseases in which bacteria are the etiological agents, particularly *Aeromonas* spp., *Flavobacterium psychrophilum*, *Pseudomonas* spp., *Vibrio* spp., and *Yersinia ruckeri*, amongst others. Numerous phages that target the principal bacterial pathogens impacting global aquaculture have been isolated, identified, and characterized in recent years. Their efficacy was evaluated in a selection of animal models, including fish, mollusks, and crustaceans, with favorable outcomes (Table 5). Several distinct advantages of employing phages from an aquaculture standpoint include, but are not limited to, the following: widespread prevalence in nature, administrative simplicity, eco-friendliness, no adverse effects, host specificity, self-limiting growth (requiring a host to replicate constantly), easily modifiable to combat newly emerging bacterial threats, and high efficiency or activity against biofilms and multidrug-resistant bacteria (Elois et al., 2023; Fabijan et al., 2023; Liu et al., 2021; Nachimuthu et al., 2021; Ramos-Vivas et al., 2021). The typically high host specificity of predatory phages offers an edge for suppressing specific bacterial pathogens (one species or even certain strains within a species) without affecting the commensal microbiota of aquatic species. One practical strategy in phage treatment is the adoption of phage cocktails (polyphage therapy) with a broad specificity spectrum to amplify the depth of activity against a diverse range of bacteria in aquaculture production (Kowalska et al., 2020; Kumari et al., 2023; Schulz et al., 2022). Thus, simultaneous treatment of distinct bacterial pathogens is feasible, promptly resulting in increased effectiveness. Scientific undertakings in the recent past have documented the discovery of potentially useful phages and the proportional application of both monophage and polyphage therapies for the eradication of aquaculture-related diseases. Nevertheless, the results varied, ranging

from the complete elimination of bacteria to the delay of disease progression and improved survival in various aquaculture species (Donati et al., 2021; Jia et al., 2020; Lomeli-Ortega, Barajas-Sandoval et al., 2023; Rorbo et al., 2018; Stalin & Srinivasan, 2017). Phages can be administered via different routes in aquaculture settings, either through oral delivery (phage-impregnated feeds), parenterally (intraperitoneally and intramuscularly), or as water additives (Liu, Han, et al., 2022; Schulz et al., 2022). Most phages can be grouped as being temperate (exhibiting a lysogenic life cycle) or lytic (exhibiting a lytic life cycle). Lytic (virulent) phages, in particular, may provide an effective intervention by lysing their specific host bacteria with immediate viral replication (Imran et al., 2023; Zia & Alkheraije, 2023). During this process, lytic phages destroy a significant proportion of bacterial cells, and such an intrinsic characteristic makes them versatile and ideal candidates for therapeutic consideration in biotechnological applications to aquaculture. Temperate (non-virulent) phages, by contrast, integrate their genomes into bacterial chromosomes and persist as either prophages or separate plasmids without killing the host (Huang et al., 2022; Xu et al., 2022; Zia & Alkheraije, 2023). Prophages may then pursue a lytic replication cycle (prophage induction) leading to the lysis of their host, most often in response to various stressors (e.g., ultraviolet radiation, nutrient starvation, DNA impairment, and antimicrobial therapy) (Schulz et al., 2022; Strathdee et al., 2023). Temperate phages are obviously poor options for therapy due to possible horizontal gene transfer of virulence factors or antibiotic resistance genes through transformation, but they can be genetically engineered to be strictly lytic, deliberately transforming them into therapeutic candidates (Lobocka et al., 2021; Meile et al., 2022; Strathdee et al., 2023). Such engineered phages can be further modified for superior lytic capability while expanding their host range to facilitate therapy (Zhou, Liu, et al., 2023). Albeit not the best bet, however, a very recent case has been described in which a novel temperate phage, vB_AbaM_ABMM1, isolated from wastewater exerted noticeable protective effects against *Acinetobacter baumannii* infection in the zebrafish model (Mardiana et al., 2023). Furthermore, to avoid the potential hazards ascribed to the use of temperate phages, as previously outlined, the application of purified phage components (e.g., endolysins or phage-encoded hydrolases) could be taken into account (Nachimuthu et al., 2021; Wang, Han, et al., 2022). While phages may infect and kill bacteria, not all bacteria are helpless or defenseless against phage invasion, as they can evolve resistance through an assortment of defense mechanisms, namely adsorption inhibition, restriction-modification, superinfection exclusion, and abortive infection systems, amongst others (Hasan & Ahn, 2022; Li et al., 2022; Torres-Barcelo et al., 2022). The "phage training" approach has been recently suggested by proponents, in which potential phages are preemptively coevolved with target bacteria to counter their host defenses (Abdelsattar et al., 2021; Borin et al., 2021; Liu, Han, et al., 2022). Hence, targeting a phage treatment must be tailored to the respective infection through both evolutionary selection and genetic engineering, and much work remains to be done in this regard.

The explosive interest in the multitude of modifications that make phages harmless and much better suited for sought-after modern therapeutic applications has led to the swift advancement of phage genetic engineering (Hibstu et al., 2022; Strathdee et al., 2023). Specific phage characteristics may work favorably for or against a particular therapeutic application. For apparent reasons, purposeful selection of natural phage isolates must fulfill particular criteria for therapeutic considerations in aquaculture, with unique attributes such as an obligatory lytic nature, virulence factors, high stability and antibacterial efficacy, antibiotic resistant determinants, the absence of toxin-encoding, and non-participation in horizontal gene transfer (Liu, Han, et al., 2022; Nokhwal et al., 2023; Schulz et al., 2022). In a concerted attempt to circumvent the therapeutic limitations of natural phages, an array of precise phage variants, well characterized at the proteomic and genomic levels, is indispensable for significant applicative implications. Notwithstanding, many other factors, including water quality

Table 5

The application of phage treatments in various animal models against bacterial pathogens in aquaculture.

Animal species	Phage	Etiologic agent	Application method	Principal response	Reference
Atlantic cod (<i>Gadus morhua</i>) and Turbot (<i>Scophthalmus maximus</i>)	KVP40 (lytic)	<i>Vibrio anguillarum</i> (strains PF430-3, 90-11-286, and 4299)	Immersion of infected fish eggs (0.5–1 CFU/mL) in seawater containing the phage (monotherapy; $0.5-8 \times 10^8$ PFU/mL) while maintaining the MOI of 5–100	↓ and/or delayed <i>Vibrio</i> -induced mortality in both fish larvae; relative mortalities for cod and turbot were ↓ by 72 % and 22–33 %, respectively	Rorbo et al. (2018)
Pond loach (<i>Misgurnus anguillicaudatus</i>)	Akh-2 (lytic)	<i>Aeromonas hydrophila</i>	Immersion of infected fish (1×10^7 CFU/mL) in water containing the phage (monotherapy; 1×10^8 PFU/mL) while maintaining the MOI of 10	↑ survival rate of infected fish; cumulative mortalities in treated groups were 16 %, 53 %, 57 %, and 56.67 % after 24, 48, 72, and 96 h, respectively, compared to the control at 100 %; most surviving phage-treated fish exhibited no apparent disease symptoms	Akmal et al. (2020)
Nile tilapia (<i>Oreochromis niloticus</i>)	PAh4 (lytic)	<i>Aeromonas hydrophila</i>	Infected fish (3.16×10^5 CFU/fish) were fed diets supplemented with the phage (monotherapy; 10^2-10^8 PFU/g diet)	↓ <i>Vibrio</i> -induced mortality of fish in a dose-dependent manner	Phumkhachorn and Rattanachaiakunsonopon (2020)
	pAh6.2 TG (lytic)	<i>Aeromonas hydrophila</i>	Immersion of infected fish in water containing the phage (monotherapy; MOI 0.1 and 1)	↑ RPS of infected fish (73 % and 50 % for MOI 1 and 0.1, respectively); significantly ↓ pathogen concentrations in both water and the fish body; ↑ IGM level in surviving phage-treated fish	Dien et al. (2022)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	FpV4 and FPSV-D22 (lytic phages)	<i>Flavobacterium psychrophilum</i>	Infected fish (1×10^4 CFU/fish) were injected intraperitoneally with a phage cocktail (polytherapy; 1.7×10^8 PFU/fish)	↑ survival rate of infected fish; survival rates in the treated and control groups were 91.4 % and 20 %, respectively; constant detection of phages in the brain, intestine, kidney, and spleen of fish	Donati et al. (2021)
Shark catfish (<i>Pangasius buchani</i>)	φAHBHU12, φAHBHU16, and φAHBHU19 (lytic phages)	<i>Aeromonas hydrophila</i>	Infected fish (8×10^5 CFU/fish) were treated with varying doses of the phage cocktail through immersion or intramuscular injection (10^5-10^8 PFU/mL)	↑ survival rate of infected fish; the highest survival rate ranged from 87 % to 100 % depending on the route of phage administration	Kumari et al. (2023)
Striped catfish (<i>Pangasionodon hypophthalmus</i>)	<i>A. hydrophila</i> -phage 2 (Φ2) and <i>A. hydrophila</i> -phage 5 (Φ5) (lytic phages)	<i>Aeromonas hydrophila</i>	Infected fish (3.2×10^6 CFU/fish) were injected intraperitoneally with a phage cocktail (polytherapy; MOI 0.01, 1, and 100)	↑ survival rate of infected fish; cumulative mortalities were 0 (MOI 100), 45 % (MOI 1), 68.3 % (MOI 0.01), and 81.7 % (positive control)	Le et al. (2018)
	PVN02 (lytic)	<i>Aeromonas hydrophila</i>	Infected fish were fed diets supplemented with the phage (monotherapy; log 4.2 and log 6.2 PFU/g diet)	↓ mortality of infected fish by 51.6 %–60 %	Dang et al. (2021)
Common carp (<i>Cyprinus carpio</i>)	IME-JL8 (lytic)	<i>Citrobacter freundii</i>	Infected fish (2×10^9 CFU fish) were injected intraperitoneally with the phage (monotherapy; 10^6-10^8)	↑ survival rate of infected fish (100 % with 10^8 PFU/mL) after 3 days; ↓ bacterial load in fish blood	Jia et al. (2020)
Common carp (<i>Cyprinus carpio</i>)	vB_AhaP_PZL-Ah1 and vB_AhaP_PZL-Ah8 (lytic phages)	<i>Aeromonas hydrophila</i> Ah-138	Infected fish (10^3-10^9 CFU/fish) were injected intraperitoneally with a single phage or phage cocktail (both mono- and polytherapy; 10^5 PFU/mL)	↑ survival rate of infected fish (100 % in the mixed-phages-treated group) after 7 days; ↓ bacterial load in fish blood	Yu et al. (2022)
Zebrafish (<i>Dario rerio</i>)	<i>E. tarda</i> -phage PETp9 and <i>V. harveyi</i> -phage PVHp5 (lytic phages)	<i>Edwardsiella tarda</i> ET9 and <i>Vibrio harveyi</i> VH5	Infected fish (<i>Edwardsiella tarda</i> at 5.99×10^6 CFU/fish or <i>Vibrio harveyi</i> at 7.86×10^7 CFU/fish) were fed diets supplemented with a phage cocktail (polytherapy; 10^5-10^8 PFU/mL with MOI 1, 10, and 100)	↑ survival rate of infected fish; survival rates ranged from 60 % to 87 % in phage-treated groups compared to the positive control at 7 %; no obvious pathological features (liver and intestinal tract) in phage-treated groups	Cui et al. (2022)
	vB_AbaM_ABMM1 (temperate)	<i>Acinetobacter baumannii</i>	Infected fish were injected intraperitoneally with the phage (monotherapy; MOI 1 and 10)	↑ survival rate of infected fish; cumulative mortalities in treated groups were 25 % (MOI 1) and 0 (MOI 10), after 24 and 72 h, respectively, compared to the control at 50 % and 75 %, respectively	Mardiana et al. (2023)
Gilthead seabream (<i>Sparus aurata</i>)	vB_VhaS_MAG7 (lytic)	<i>Vibrio harveyi</i> MM46	Immersion of infected fish larvae (10^6 CFU/mL) in seawater containing the phage suspension	↑ survival rate of infected fish larvae	Droubogiannis et al. (2023)

(continued on next page)

Table 5 (continued)

Animal species	Phage	Etiologic agent	Application method	Principal response	Reference
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	VallY-3, VspDsh-1, VspSw-1, VpaJT-1, and ValSw4-1 (lytic phages)	<i>Vibrio</i> sp. Va-F3	(monotherapy; 10^8 PFU/mL; MOI 10) Infected shrimp (2×10^6 CFU/mL) were treated with a phage cocktail (polytherapy; 2×10^7 PFU/mL)	↑ survival rate of infected shrimp; survival rates in the treated and control groups were 91.4 % and 20 %, respectively, after 7 days	Chen et al. (2019)
	AL-2 (lytic)	<i>Vibrio parahaemolyticus</i> M0904	Immersion of infected shrimp (8×10^4 CFU/mL) in culture medium containing the phage (monotherapy; 2.69×10^5 PFU/mL)	↓ mortality in infected shrimp; phage-treated shrimp exhibited a 3-h delay in acute phase mortality	Gonzalez-Gomez et al. (2023)
Brine shrimp (<i>Artemia franciscana</i>)	vB_Vc_SrVc9 (lytic)	<i>Vibrio campbellii</i>	Immersion of infected brine shrimp in culture medium containing the phage (monotherapy)	↑ survival in brine shrimp by 24 %; ↓ presumptive <i>Vibrio campbellii</i> to non-detectable numbers	Lomeli-Ortega et al. (2021)
Blue mussel (<i>Mytilus edulis</i>)	VP10 phage cocktail (containing 12 lytic phages)	<i>Vibrio parahaemolyticus</i>	Infected mussels (10^9 CFU/mL) were treated in seawater containing the phage cocktail (polytherapy; 0.1×10^6 PFU)	↓ <i>Vibrio parahaemolyticus</i> to undetectable numbers in mussels, seawater, and sediment after 48 h	Onarinde and Dixon (2018)
Pacific oyster (<i>Crassostrea gigas</i>)	pVco-14 (lytic)	<i>Vibrio coralliilyticus</i>	Immersion of infected larvae (10^3 – 10^6 CFU/mL) in seawater containing the phage (monotherapy; 10^4 – 10^7 PFU/mL)	↑ survival rate in larvae; cumulative mortalities ranged from 6.06 % to 21.77 % in phage-treated groups compared to 42.86 %–81.44 % in the untreated control	Kim et al. (2019)
Rock oyster (<i>Saccostrea glomerata</i>)	Φ-5, Φ-6, and Φ-7 (lytic phages)	<i>Vibrio alginolyticus</i>	Infected larvae (10^5 CFU/mL) were treated in seawater containing a phage cocktail (polytherapy; 10^8 PFU/mL)	↓ mortality in larvae by almost 50 % (28.2 % in phage-treated groups and 77.9 % in the control) after 24 h incubation	Le et al. (2020)

Abbreviations: MOI, multiplicity of infection; RPS, relative percent survival.

(physicochemical parameters), timing and route of administration, and phage concentration and kinetics, amongst others, are to be given close and thoughtful attention for successful preventive treatment in the field, as comprehensively reviewed elsewhere (Kowalska et al., 2020; Liu, Han, et al., 2022; Zaczek et al., 2020). Simply put, while the correct employment method is critical, disparities exist for each biological system, particularly outdoor facilities that are exposed to natural fluctuations and should be scrutinized independently. Nonetheless, phage therapy for aquaculture is still in the research phase, and more in-depth explorations are crucial to justifying its efficacy for large-scale applications. Such practices should also be considered for their potential effects on the aquatic environment as a whole.

7. Challenges to ponder for practical field implementation

Aquaculture is best positioned to address food security and economic progress. Accordingly, solid aquaculture practices integrated with highly promising biological strategies underpin the fundamental actions that would ensure production success. Despite the well-established nature of various biological control measures as intrinsic components of aquatic health management, they are not without obstacles when it comes to practical implementation. Since every aquaculture facility operates differently, such an aspect must be accounted for when considering the most suitable biocontrol strategy. Undoubtedly, the many benefits of biocontrol measures could vary substantially with regard to the species being raised, culture conditions, and other unforeseen elements. Numerous factors, viz., husbandry practices, environmental fluctuations, intervention regimes, and host genotypes, are primary sources of heterogeneity, markedly contributing to outcome discrepancies. For this reason, aquaculture operations must seek out (through science) and deploy biological tools that perform satisfactorily under the specific conditions associated with each facility and the large cohort of cultivated species. Another pertinent issue is the interaction of environmental stressors and co-infections that trigger the emergence or manifestation of diseases (Okon et al., 2023; Wise et al., 2021), which might hamper successful outcomes altogether. This is when things turn muddled and complicated for most farmers or aquaculture practitioners,

as the best approach is not always identifiable or decidable in the prevention and control of aquatic diseases. Additionally, the technology transfer of some biological approaches (e.g., phage therapy and QSI) to the wider industry remains a big hurdle due to insufficient grasp and poor marketing strategies. Furthermore, though functional feed ingredients (i.e., probiotics, prebiotics, synbiotics, paraprobiotics, postbiotics, and phytochemicals) offer impressive health benefits, their successful application or efficacy and broad impacts are conceivably unpredictable, given the presently vague or insufficient understanding of proper dosing, supplementation strategies, the function of stress (biotic and abiotic), and the complexity of biological systems with respect to the diverse variety of aquaculture species. Moreover, immunostimulants may not be effective against all pathogenic diseases, and regular and prolonged provision of such substances at excessive dosages does not necessarily confer continuing benefits (Van Doan et al., 2022; Vijayaram et al., 2022). Notwithstanding significant progress in the field, many uncertainties remain, such as the toxicity and safety of some biological preparations (e.g., phytochemical extracts and bacteriophage) (Firmino, Galindo-Villegas, Reyes-Lopez, & Gisbert, 2021; Kowalska et al., 2020; Liu, Han, et al., 2022). Nonetheless, given the renewed interest and enthusiasm coupled with the advent of novel technologies, there is reason to believe that these challenges can be surmounted in future years.

8. Conclusion and future outlook

A key impediment to the production of many aquaculture species is the emergence of infectious diseases. Antimicrobial resistance is one of the primary threats to global food security and public health systems, which arises when etiological agents develop resistance to therapeutic drugs. Aquaculture operations are not impervious to this danger, seeing that antimicrobials have been extensively utilized to safeguard aquatic species against diseases. Thus, ideal and contemporary strategies to restrain the development of AMR are the need of the hour. The prophylactic use of various promising and novel biological control methods, including high-value functional components (e.g., probiotics, prebiotics, synbiotics, paraprobiotics, postbiotics, and phytochemicals), phage therapy,

and QSI, is rising with the demands for environmentally sound and sustainable alternatives for integrated aquatic disease management. A profound understanding of their modes or mechanisms of action serves as the basis for rational selection and application in aquaculture production. It is, however, crucial to continue developing a wide range of strategies that could be employed in rotation or combination in a biological control program since it is unlikely that any single approach will always be practical and effective in all circumstances. Within this context, continuous refinement and adaptation of these strategies are much needed if their full potential is to be realized. More in-depth and rigorous studies are still necessary to pinpoint their beneficial impacts on aquatic animal health with reference to the consistency of field conditions (e.g., weather and atmospheric variables), duration of effects, the perfect timing and route of administration, as well as the explicit functional collaborations with immunity. Much effort still has to be invested in terms of interactions with associated pathogenic communities and animal microbiomes. Advances and notable accomplishments in multi-omics technologies, i.e., metagenomics, metatranscriptomics, and metabolomics, should assist in accomplishing these goals toward a greener and more sustainable blue revolution for the benefit of animals, society, and the environment as a whole, duly conforming in all respects to the "One World, One Health" (OWOH) Joint Plan of Action.

CRedit authorship contribution statement

Keng Chin Lim: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Fatimah Md Yusoff:** Writing – review & editing, Visualization, Validation, Supervision, Conceptualization. **Fatin M.I. Natrah:** Visualization, Validation, Resources, Funding acquisition. **Mahanama De Zoysa:** Writing – review & editing, Visualization, Validation. **Ina Salwany Md Yasin:** Writing – review & editing, Visualization, Validation. **Jasmin Yaminudin:** Writing – review & editing. **Murni Karim:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of generative AI use in scientific writing

This manuscript was prepared with the assistance of generative artificial intelligence (AI) tools, to aid in drafting and language refinement. The AI-generated content was reviewed, edited, and validated by the authors to ensure accuracy, originality, and compliance with ethical and scientific standards.

The authors take full responsibility for the final content of the manuscript and affirm that the AI was not used for data analysis, interpretation, or any aspect requiring scientific judgment beyond language assistance.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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