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**β-GLUCANS AS NATURAL IMMUNOSTIMULANTS IN AQUACULTURE
(review)**

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Aquaculture is one of the fastest-growing sectors of global food production; however, the intensification of farming practices has resulted in increased disease prevalence, elevated stress levels in cultured fish and a growing dependence on antibiotics. These challenges highlight the urgent need for sustainable, environmentally safe and biologically effective alternatives for health management in aquaculture systems. **Objective** of this review was to analyse the immunostimulatory potential of β-glucans as natural feed additives in aquaculture, with particular emphasis on their mechanisms of action, physiological effects and practical applicability in intensive fish farming. **Methods** applied included a critical analysis and synthesis of experimental and review studies published in international peer-reviewed journals, focusing on molecular, cellular and organism-level responses of fish to β-glucan administration. Data concerning β-glucan structure, receptor-mediated recognition, immune signalling pathways and functional outcomes were systematically evaluated. **Results** demonstrate that β-glucans significantly enhance innate and adaptive immune responses in fish through activation of macrophages, neutrophils and other immune effector cells via pattern recognition receptors, including C-type lectins, complement-related receptors and Toll-like receptors. Their administration leads to increased phagocytic activity, cytokine production and improved resistance to bacterial, viral and parasitic infections. In addition to immune modulation, β-glucans positively influence growth performance, antioxidant capacity, gut health and stress resilience under intensive aquaculture conditions. Evidence also suggests the induction of long-term functional reprogramming of innate immune cells, known as trained immunity, which may contribute to prolonged non-specific protection in teleost fish. **Conclusions** indicate that β-glucans represent one of the most promising natural immunostimulants for sustainable and antibiotic-free aquaculture. Nevertheless, variability in β-glucan sources, molecular structures, dosages and delivery methods remains a critical limitation. Further standardisation and advanced transcriptomic, proteomic and metabolomic studies are required to optimise their application and fully elucidate immune–endocrine interactions in fish.

Key words: β-glucans, aquaculture, fish immunity, immunostimulation, functional feeds, disease resistance, sustainable production

Introduction. Between 2010 and 2030, aquaculture is expected to grow by 62 %, meeting over two-thirds of the global demand for fish and shellfish [1]. Around 100 million people depend on this sector for their livelihoods, highlighting its socio-economic importance [2]. In addition to its role in ensuring food security and reducing poverty – in line with the UN's 2030 Sustainable Development Goals – aquaculture also provides ecosystem services such as wastewater treatment and habitat restoration [1]. However, these benefits depend on sustainable practices. Poor management can deplete water resources, intensify overfishing, introduce invasive species and accelerate antimicrobial resistance [3]. The rapid expansion of aquaculture must be matched by robust environmental and health safeguards to ensure long-term viability.

A major barrier to growth is the prevalence of aquatic diseases, exacerbated by global trade, climate change and intensification of farming systems [4]. High-density farming promotes the evolution of pathogens and outbreaks, often leading to the heavy use of antibiotics and disinfectants. Yet overuse of these substances weakens immune systems and fosters resistant bacteria, posing risks to both animal and human health [5]. Residual antibiotics in fish meat and environmental contamination further compound these issues [1]. This highlights the need for integrated health management strategies that reduce reliance on chemicals while safeguarding productivity.

Maintaining fish health under intensive conditions remains a persistent challenge. Elevated stocking densities increase stress and disease susceptibility. With the use of antibiotics now restricted or banned in many regions, alternative immune-boosting approaches are essential [1]. One promising solution is the use of β -glucans, which are natural immunostimulants that have been tested in fish for decades. They are safe, effective and environmentally friendly, offering a viable path towards sustainable aquaculture health management [6].

Historical overview and mechanistic background. The β -glucan molecule was first described in 1946 by Dimler et al., who isolated D-glucosan (1,4)(1,6)- β -glucan from starch [7]. Nearly two decades later, Wooles and DiLuzio [8] provided compelling evidence of its immunomodulatory properties. Their study in the journal *Science* showed that β -glucan injections in mice enhanced phagocytic activity and boosted both primary and secondary immune responses. This discovery paved the way for decades of research confirming the broad immunostimulatory potential of β -glucans across species [9].

Subsequent studies have demonstrated the positive effects of β -glucans on immune responses in various species, including mammals such as humans, dogs, pigs, cattle, horses, and sheep; birds such as chickens; amphibians such as frogs; fish; and invertebrates such as shrimp, crabs, and insects including bees and *Drosophila* [9]. These findings underscore the evolutionary conservation of β -glucan recognition mechanisms.

Their cross-species efficacy is linked to conserved immune pathways, particularly those involving pathogen-associated molecular patterns (PAMPs). In this context, fish, being the earliest vertebrates with adaptive immunity, offer a unique opportunity to study the interface between innate and adaptive

responses [5]. This makes fish an excellent model for investigating β -glucan-mediated immune activation and its implications for aquaculture, particularly in the development of functional feeds and sustainable health strategies.

β -Glucans in aquaculture: structure, function and application.

β -glucans are polysaccharides composed of β -D-glucose units linked together in a specific order. They are found in the cell walls of bacteria, fungi, microalgae, and cereals (Fig. 1). Their structure, typically a β -1,3-linked backbone with β -1,6 branches, varies by source. This influences their molecular mass, solubility, and physiological effects. These structural differences are key to their biological activity [6, 9].

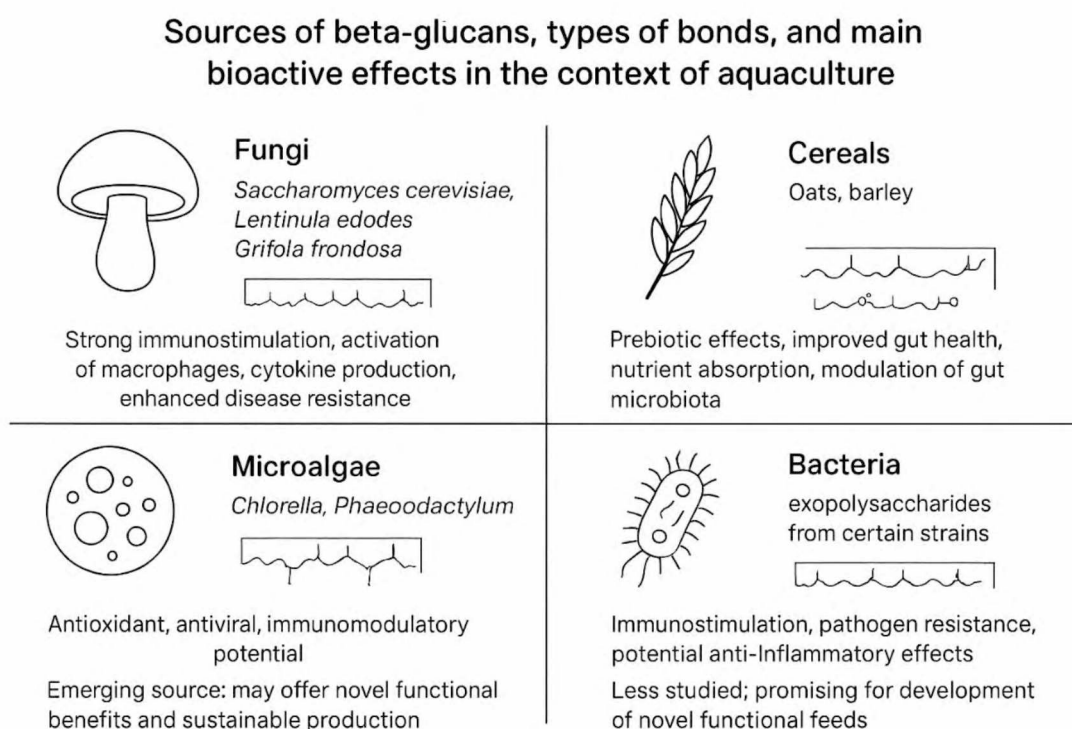


Fig. 1. Sources of beta-glucans (fungi, cereals, microalgae and bacteria), chemical structures and bioactive effects in the context of aquaculture.

In aquaculture, they are commonly used as feed additives to enhance immunity, improve disease resistance and support growth. They stimulate immune cells such as macrophages and neutrophils, thereby strengthening both innate and adaptive responses against parasites, viruses and bacteria. They also promote gut health by supporting beneficial microbiota, lowering intestinal pH and reducing harmful metabolites. These combined effects contribute to better feed efficiency and sustainability [1, 6, 9].

β -glucans are potent stimulators of cellular and humoral immunity in mammals, invertebrates and fish. They are best known for enhancing phagocytosis by granulocytes, macrophages and dendritic cells (DCs), which play a key role in host defence. During microbial degradation, pathogen-associated molecular patterns (PAMPs) activate antigen-presenting cells and

naïve T cells, triggering inflammatory responses via receptor binding and intracellular signaling [6, 9].

The initial step in the interaction between β -glucans and immune cells involves binding to pattern recognition receptors (PRRs) on the cell membrane. Key receptors include TLR-2, dectin-1, CR3 (CD11b/CD18), lactosylceramide and scavenger receptors [10–12]. CR3, a multifunctional receptor found on myeloid cells, mediates β -glucan binding and activates the Syk pathway, resulting in CR3-dependent cytotoxicity (CR3-DCC) [13, 14].

Dectin-1, another major receptor, is critical for antifungal immunity and cytokine regulation. It promotes IL-12 production and IFN- γ secretion by NK cells [15, 16]. Recently, attention has shifted to Toll-like receptors (TLRs), particularly TLR-2, which interact with β -glucans such as curdlan to modulate immune responses, including the suppression of RANKL expression [17].

The immune response depends on β -glucan solubility and structure. Insoluble forms cluster dectin-1 receptors, displacing inhibitory molecules such as CD148 and CD45, and initiating signalling cascades [18]. Some β -glucans bind to both dectin-1 and TLRs, forming receptor complexes that fine-tune immune activation. Dectin-1 cooperates with TLRs 2, 4 or 6, and the biological outcome varies with receptor combinations and glucan solubility [19].

In addition to classical immune activation, β -glucans influence immune checkpoints. They reduce the expression of the c-Maf transcription factor in M2 macrophages and shift monocyte populations towards the classical 'patrolling' types that regulate tumour metastasis [20]. There is emerging evidence to suggest the involvement of the PD-1 signalling pathway, which expands the therapeutic potential of β -glucans to include cancer immunotherapy.

Although the exact mechanisms of β -glucan activity in fish are not yet fully elucidated, they appear broadly similar to those in mammals due to the evolutionary conservation of innate immunity. In salmon macrophages and catfish neutrophils, complement protein C3 and lectins – likely C-type lectin receptors (CLRs) – have been identified as β -glucan recognition molecules [21]. Gene expression studies in carp suggest that β -glucans activate signaling pathways typical of the CLR family [22].

In addition, TLR homologues have been identified in several fish species, including salmon, zebrafish, and flounder [23], indicating a conserved TLR-mediated recognition mechanism. However, no direct dectin-1 homologue has been confirmed in teleost genomes. While carp possess over 200 genes encoding C-type lectin domains, none have been definitively linked to β -glucan binding [22]. Still, β -glucans like curdlan – known to bind dectin-1 in mammals – trigger similar immune responses in fish, suggesting the presence of functionally analogous receptors.

There is also indirect evidence for CR3-like receptors in fish macrophages. Although their molecular identity remains unclear, zebrafish genomes contain candidate genes with similar domain structures, supporting the idea of conserved β -glucan-binding PRRs in fish [22]. This highlights the evolutionary continuity of innate immune recognition and the potential for β -glucans to modulate fish immunity via multiple receptor pathways.

In addition to binding to receptors, β -glucans modulate the expression of immune-related genes and signalling proteins, thereby influencing both innate and adaptive responses. In the macrophages of salmon and trout, exposure to

β -glucans was found to upregulate cytokines such as IL-1 β , IL-6 and TNF- α , though not complement C3 [24]. Similar effects were observed in tilapia plasma [25].

These transcriptional changes can occur rapidly. Short-term immersion (four 45-minute sessions per week) increased the expression of IL-1 β , TNF- α , IL-6, IL-10 and TGF- β , sometimes following a single exposure [26]. In carp infected with haemorrhagic virus, β -glucan pre-treatment elevated MX antiviral gene expression during the early stages of infection [27]. Similarly, in cod challenged with *Vibrio anguillarum*, β -glucan immersion increased IL-1 β and IL-10 expression in intestinal tissues. The addition of mannan-oligosaccharides further increased IL-8 and IFN- γ levels, suggesting a synergistic effect [28]. β -glucan exposure has also led to the discovery of new immune genes. In carp, two β -defensins and mucin-related genes were upregulated following treatment [29]. In fish infected with *Aeromonas salmonicida*, dietary β -glucans reduced pro-inflammatory cytokines, suggesting an anti-inflammatory effect during infection [30]. Long-term (25-day) supplementation in carp significantly increased the expression of iNOS, Bcl-2, Nemo, caspase-9 and p38 MAPK – genes linked to apoptosis and cell survival [31]. These findings suggest that β -glucans activate immune signalling and regulate apoptosis and oxidative stress, thereby enhancing immune resilience. Despite these insights, our genomic understanding of β -glucan action remains limited. Comprehensive transcriptomic and proteomic studies are essential to uncover receptor diversity, signalling pathways, and innate–adaptive immune cross-talk in teleost fish.

Broader physiological and practical relevance of β -glucans in fish aquaculture. Beyond immune stimulation, β -glucans influence a wide array of physiological processes. For example, in a 60-day study with rainbow trout (*Oncorhynchus mykiss*), proteomic analysis revealed changes in muscle protein expression, which could explain the improved growth and feed efficiency observed in the supplemented groups [32].

The benefits of β -glucans extend to nutritional and stress-mitigating effects. In Nile tilapia (*Oreochromis niloticus*), for example, β -glucans counteracted deltamethrin toxicity by normalising cortisol levels and reversing disturbances to inflammatory genes [33]. In *Pangasianodon hypophthalmus*, supplementation reduced mortality due to cold stress [34], while in *O. mossambicus*, it enhanced cellular, humoral and antioxidant defences in response to ammonia stress [35].

These results suggest that β -glucans act as pleiotropic modulators, affecting immunity, metabolism, and oxidative balance. Their mechanisms likely involve receptor signalling and indirect regulation of stress hormones, possibly via the neuroendocrine–immune axis (Fig. 2). Although data on fish are limited, studies on mammals show that cytokines and neuropeptides interact with the hypothalamic–pituitary–adrenal (HPA) axis, thereby influencing the release of hormones and immune activity [9]. This opens up a promising avenue for future research in teleost fish, focusing on how β -glucans may support neuroendocrine regulation and enhance resilience under aquaculture stressors.

BROAD PHYSIOLOGICAL AND PRACTICAL RELEVANCE OF β -GLUCANS IN FISH AQUACULTURE

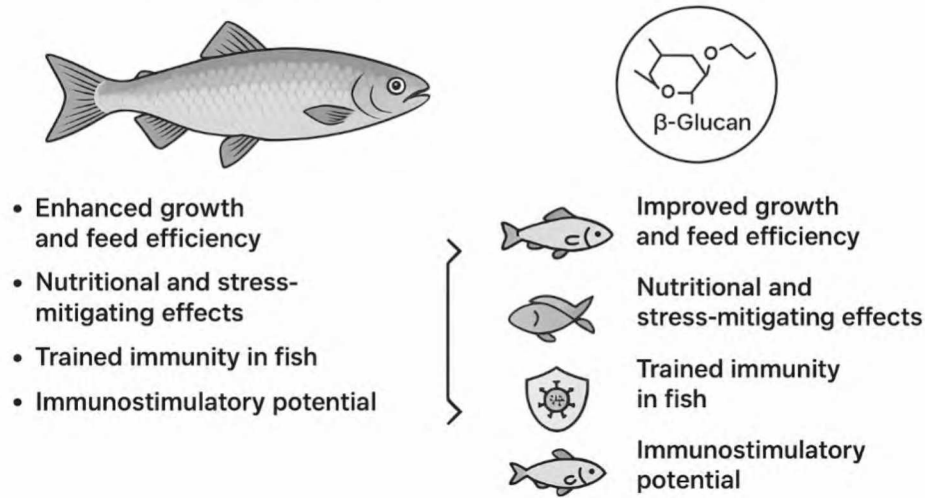


Fig. 2. Broader physiological and practical relevance of β -glucans in fish aquaculture

Recent immunological findings suggest that β -glucans may induce the long-term reprogramming of innate immune cells, a process known as 'trained immunity' [36]. Unlike the traditional view of innate immunity as memoryless, trained immunity meets three criteria: (i) protection after primary exposure without T or B cell involvement; (ii) enhanced non-specific resistance; and (iii) mediation by macrophages, NK cells and other innate effectors [37]. A well-known example of this is the non-specific protection provided by BCG vaccination, which activates macrophages and improves resistance to unrelated pathogens [38]. Similar memory-like responses have been observed in plants [39] and invertebrates [40], despite the absence of adaptive lymphocytes in these organisms. Given the evolutionary position of teleost fish as early vertebrates, it is plausible that comparable mechanisms exist in fish [36].

Evidence is accumulating. In brook trout (*Salvelinus fontinalis*), for example, macrophages showed enhanced phagocytic activity up to 33 days after exposure to *Mycobacterium butyricum* [41]. Similarly, BCG vaccination in Japanese flounder and amberjack has been shown to induce cross-protection against unrelated pathogens, with increased cytokine expression and serum bacteriolytic activity [42]. One particularly compelling study in Rag-knockout zebrafish, which lack adaptive immunity, showed that prior exposure to *Edwardsiella ictaluri* provided protection against a lethal challenge. Transferring kidney leukocytes from exposed fish protected naïve individuals, indicating innate immune memory [43]. These findings suggest that trained immunity may operate in teleosts, but further research is needed to confirm its prevalence and clarify the role of macrophages as central mediators [36].

Immunostimulatory potential of β -glucans in aquaculture. Of the various immunostimulants tested in aquaculture, β -glucans have proven to be the most consistently effective and practical [44]. The benefits of β -glucans, including enhanced survival, immune activation and disease resistance, have been

confirmed across numerous species, including *Oncorhynchus mykiss*, *Salmo salar*, *Cyprinus carpio*, *Oreochromis niloticus* and *Danio rerio* [6].

In carp, for example, β -glucans administered via injection, bathing or feeding increased survival by stimulating superoxide production, IL-1 secretion and antibody formation [45]. In trout, treated macrophages exhibited stronger bactericidal activity against *A. salmonicida* [46], and radiolabelling studies confirmed the intestinal uptake and systemic clearance of β -glucan particles [47].

β -glucans also act as vaccine adjuvants, enhancing antibody titres and cytokine responses in salmon vaccinated against vibriosis and yersiniosis [48–50]. Co-supplementation with vitamins C and E has also been shown to further improve macrophage function [51]. However, outcomes vary depending on dosage, delivery method, and glucan structure. Notably, only β -(1,3/1,6)-glucans provided significant protection against *A. hydrophila*, highlighting the need for structural standardisation.

Beyond bacterial infections, β -glucans exhibit antiviral effects, reducing mortality from viral haemorrhagic septicaemia, and antiparasitic activity, lowering the prevalence of *Ichthyophthirius* and *Dactylogyrus* in trout and snappers [6]. These findings confirm their ability to modulate both innate and adaptive immunity for broad-spectrum protection. Despite extensive research, optimal application strategies regarding structure, dosage and delivery remain to be standardised. Nevertheless, the combined immunostimulatory, antioxidant and stress-buffering effects of β -glucans make them one of the most promising tools for enhancing the health and resilience of fish in intensive aquaculture.

Conclusions. Aquaculture is one of the fastest-growing food production sectors and plays a pivotal role in ensuring global food security and sustainable livelihoods. However, the intensification of production has also led to an increase in the frequency and severity of infectious diseases, highlighting the urgent need for effective and environmentally friendly immunostimulants. Of the various alternatives explored, β -glucans have emerged as the most reliable and versatile natural compounds capable of enhancing disease resistance, growth performance and stress resilience in fish.

Their immunomodulatory effects, mediated through pattern recognition receptors such as CR3, TLRs, and C-type lectins, promote both innate and adaptive immune responses. β -glucans also modulate gene expression linked to cytokine production, apoptosis, and oxidative stress regulation, resulting in improved overall fish health. Furthermore, their pleiotropic benefits extend beyond immunity to include metabolic balance, gut homeostasis, and neuroendocrine stress adaptation.

Despite substantial evidence supporting their efficacy, further standardisation of β -glucan sources, structures, and delivery methods is required to ensure consistent outcomes across aquaculture species. Advanced transcriptomic, proteomic and metabolomic analyses are essential for elucidating receptor diversity and the signalling pathways involved in β -glucan-mediated immunity. Thus, β -glucans are key to the development of sustainable and antibiotic-free aquaculture, in line with global efforts to improve fish welfare, protect the environment, and ensure food safety.

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β-ГЛЮКАНИ ЯК ПРИРОДНІ ІМУНОСТИМУЛЯТОРИ В АКВАКУЛЬТУРІ (оглядова)

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Аквакультура є однією з галузей світового виробництва продуктів харчування, що зростає найбільш динамічно; проте інтенсифікація сільськогосподарських практик призвела до збільшення випадків розповсюдження захворювань, підвищення рівня стресу у вирощуваних риб та зростання залежності від застосування антибіотиків. Ці виклики підкреслюють нагальну потребу в стійких, екологічно безпечних та біологічно ефективних альтернативах для управління здоров'ям в системах виробництва аквакультури. **Метою** цього огляду був комплексний аналіз потенціалу використання в аквакультурі β-глюканів як природних кормових добавок, що стимулюють імунітет, з особливим акцентом на механізмах їх дії, фізіологічні ефекти та практичне застосування в інтенсивному рибництві. **Методи** досліджень включали критичний аналіз та синтез даних експериментальних досліджень та оглядових статей, опублікованих у міжнародних рецензованих журналах, з акцентом на молекулярні, клітинні та організмові реакції риб на введення β-глюканів. Було систематично оцінено дані щодо структури β-глюканів, рецепторного розпізнавання, імунних сигнальних шляхів та функціональних результатів. **Результати** аналізу показують, що β-глюкани суттєво посилюють вроджені та адаптивні імунні реакції у риб шляхом активації макрофагів, нейтрофілів та інших імунних ефektorних клітин через рецептори розпізнавання патернів, включаючи лектини типу С, рецептори, пов'язані з комплементом, та Toll-подібні рецептори. Їх введення призводить до підвищення фагоцитарної активності, вироблення цитокінів та поліпшення стійкості до бактеріальних, вірусних та паразитарних інфекцій. Окрім імуномодуляції, β-глюкани позитивно впливають на показники росту, антиоксидантну здатність, здоров'я кишечника та стійкість до стресу в умовах інтенсивних технологій вирощування аквакультури. Проаналізовані дані також свідчать про індукцію довгострокового функціонального перепрограмування клітин вродженого імунітету, відомого як тренований імунітет, що може сприяти тривалому неспецифічному захисту костистих риб. **Висновки:** β-глюкани є одним з найперспективніших природних імуностимуляторів для сталого вирощування аквакультури без використання антибіотиків. Проте варіативність джерел β-глюканів, їх молекулярних структур, дозувань та методів доставлення залишається критичним обмеженням. Для оптимізації їх застосування та повного з'ясування імуно-ендокринних взаємодій в організмі риб необхідно провести подальшу стандартизацію та поглиблені транскриптомні, протеомні та метаболомні дослідження.

Ключові слова: β-глюкани, аквакультура, імунітет риб, імуностимуляція, функціональні корми, стійкість до хвороб, стале виробництво

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Автори рукопису засвідчують, що у процесі проведення дослідження та підготовки цього рукопису для виконання будь-яких завдань не використовували жодних інструментів або сервісів генеративного ШІ, перелічених у Таксономії делегування завдань генеративному ШІ (GAIDeT, 2025). Усі етапи роботи виконані виключно авторами.

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