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Review Article

Role of exogenous bile acids in unlocking the potential of nutritional bio-energetics of freshwater aquaculture

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Abstract

The growing intensity of freshwater aquaculture poised significant burden on fish's digestive and hepatobiliary systems, which is exacerbated by the increased usage of lipids, carbohydrates, and plant-based proteins towards the goal of fish meal replacement or protein sparing, in general. Exogenous bile acids (BAs) act as physiological detergents, enabling lipid digestion and absorption, as well as key signalling molecules that regulate lipid and glucose homeostasis. BAs effectively reduce the harmful physiological effects of poor diets by lowering hepatic lipid levels, serum triglycerides, and total cholesterol. They also boost hepatic antioxidant capacity and improve immunological function. The efficiency of BAs is mostly determined by the fish species, fundamental diet, and integration rate. Importantly, BAs exhibit dose-dependent toxicity. Overdosing can have serious consequences in animals like genetically modified farmed tilapia, including stunted growth, impaired liver function (nuclear migration and vacuolization), and the promotion of gallstone formation. Accurate dosage evaluation is thus critical for effective and sustainable deployment. The present study made an insight from numerous studies that propose the use of bile acids in economically important freshwater aquaculture species like carp, tilapia, catfish, etc. From the available literatures, it emerged that the future research should focus on understanding the molecular mechanisms at work, relationships with other feed ingredients, long-term effects, and species-specific needs for safe food production of fish origin.

Keywords: Bile acids, Exogenous bile salts, Freshwater aquaculture, Immunity, Nutritional efficiency

Highlights

- Exogenous bile acids as an additive for profitable and sustainable freshwater fish farming
- Problems of using high-cost fish meal and higher level of dietary lipid and carbohydrates
- The way exogenous bile acids exert their effects
- Effects of exogenous bile acids on different freshwater fish species

INTRODUCTION

Freshwater aquaculture is of paramount global importance, regularly leading in overall aquaculture output. In 2022, inland aquaculture constituted 62.6% of farmed aquatic animals (Food and Agriculture Organization [FAO], 2024), with forecasts indicating that freshwater species, including carp, catfish, and tilapia, will represent over 62% of global aquaculture production by 2030 (FAO, 2020). This industry is essential for global food security and nutrition, supplying a crucial source of protein and micronutrients, particularly for rural people and at-risk groups in emerging nations, and is especially vital for landlocked countries. Moreover, freshwater aquaculture serves as a crucial economic catalyst, generating income and employment prospects across its value chain, aiding smallholder farmers and fostering rural development efforts in areas such as Asia and Africa.

Aquaculture, the fastest-growing sector in food production, mostly driven by freshwater resources, is essential for satisfying the rising demand for aquatic products in the context of stagnant or decreasing capture fisheries (FAO, 2018). In freshwater aqua farming, feed constitutes the predominant operational expenditure (60-70%); hence, its quality and management significantly influence economic viability, operational efficiency, environmental compliance, animal health, and the quality of the final output. Protein is the costliest nutrient in fish feed. In

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contrast to carnivorous fish, omnivorous and herbivorous warm-water fish can metabolize carbohydrates as an energy source and can withstand higher carbohydrate diets (Elshenawy et al., 2020). In general, protein sparing is a method in fish nutrition that involves using non-protein energy sources, primarily lipids and carbohydrates, to guarantee that expensive dietary protein is saved for growth, maintenance, and body protein synthesis rather than being catabolized for energy (Bhusare et al., 2023). While the majority of fish species make good use of lipids, eating too many lipids at once can stunt growth and make fish that are too obese. The opposite is also true: a lack of lipids in fish food may hinder development and immunity. Excessive carbohydrate consumption, like fat, can also disrupt fish metabolism and have a negative impact on their health (Li et al., 2024c).

Maximizing growth and sustainability in aquaculture thus requires high-quality, digestible feeds, and as aquaculture moves toward more economical and sustainable diets, premium marine ingredients like fishmeal (FM) and fish oil (FO) are frequently swapped out for plant-based sources. This alteration can adversely impact fish health and development. Plant proteins may possess anti-nutritional components that might diminish fat digestion and induce intestinal inflammation. Moreover, elevated inclusion levels of lipids or carbohydrates, employed to attain a "protein-sparing effect," frequently result in metabolic disorders, excessive hepatic lipid accumulation (fatty liver disease), and impaired immune function in the cultured fish, particularly in carnivorous freshwater species such as largemouth bass (Kamalam et al., 2017; Wang et al., 2023). Taking into consideration some recent works including a meta-analysis (Romano et al., 2020, Wang et al., 2023, Bhusare et al., 2024; Li et al., 2024c), present work concentrates on the information gathered from many research that could point our freshwater aquaculture industry in the right direction by recommending the use of bile acids in economically significant freshwater species for safe food production of animal origin.

Bile acid biochemistry

Bile acids (BAs) are essential sterol molecules characterized by their amphipathic characteristics. Bile's fundamental constituents are generated predominantly in the liver from cholesterol (Abdel-Tawwab et al., 2023). The biochemistry of bile acids encompasses their intricate structure, production mechanisms, effective enterohepatic circulation, essential physiological roles in digestion and signalling, and taxonomic variety. A 19-carbon steroid nucleus makes up BAs. It is made up of four carbon rings that are fused together: three 6-carbon rings and one 5-carbon ring (Hagey et al., 2010; Chiang, 2013). The nucleus is completely filled, unlike cholesterol. It can be cis (bent shape, found in many C24 BAs, including cholic acid, CA, and chenodeoxycholic acid, CDCA) or trans (extended/planar shape, found in basal vertebrates like hagfish)(Hagey et al., 2010). To make BAs more soluble and ionized at physiological pH, they are attached to the amino acid taurine or glycine (Chiang, 2013; Wang et al., 2023). This procedure also stops Ca^{2+} from settling out and makes passive absorption less likely. Almost all of the BAs in teleost fish are linked to taurine (Liao et al., 2020; Wang et al., 2023). The liver makes primary BAs (such CA and CDCA), and gut microbiota makes secondary BAs from primary BAs (Wahlström et al., 2016). Deconjugation (mediated by bile salt hydrolase, BSH) and 7α-dehydroxylation are two important microbiological transformations (Wang et al., 2023). Deconjugation changes CA into deoxycholic acid (DCA) and CDCA into lithocholic acid (LCA). These bio-transformations usually make the BA pool more varied and less water-soluble (Chiang, 2013; Wahlström et al., 2016; Wang et al., 2023). BAs are released into bile, which is often retained in the gallbladder. After eating, they are released into the intestinal lumen to help with digestion (Abdel-Tawwab et al., 2023; Wang et al., 2023). The entero-hepatic circulation works quite well, and over 95% of BAs are taken back up in the terminal ileum. The liver makes up for the minimal quantity lost in faeces by making new ones, keeping the BA pool steady (Chiang, 2013; Wang et al., 2023).

Mechanism of action and key benefits of bile acids

Exogenous BAs imitate endogenous BAs, which are mostly made from cholesterol in the liver. They work in two ways: as physiological detergents to help the body absorb nutrients and as signalling molecules that control metabolism and immunological responses. Therefore, the utilization of exogenous BAs as a dietary supplement, especially in aquaculture, is substantiated by a thorough array of mechanisms and corresponding advantages that encompass digestion, lipid and glucose metabolism, antioxidant defence, and immune enhancement.

Digestive mechanism: BAs, being the amphipathic sterols, have both hydrophilic and lipophilic

characteristics. They are regarded as natural fat emulsifiers and the primary constituents of bile (Alrefai & Gill, 2007). BAs cause dietary lipids to emulsify in the intestinal lumen, which results in the formation of water-soluble complexes and tiny chylous particles (Zhou et al., 2018a). By expanding the contact surface area of lipids, this action allows digestive enzymes to reach them more easily (Ding et al., 2020; Romano et al., 2020). The digestion, transportation, and absorption of fats and fat-soluble vitamins are all made easier when mixed micelles are formed. In order to improve digestion, BAs activate lipases found in the pancreas (Wang & Hartsuck, 1993; Adhami et al., 2017; Romano et al., 2020; Li et al., 2021). These lipases then catalyze the breakdown of ester bonds in fats, which aids in the digestion of fats. In addition, they have the capacity to facilitate the digestion and assimilation of dietary proteins by improving the hydrolytic capabilities of proteases that are found in the pancreas (Gass et al., 2007). Dietary supplementation with BA results in better feed efficiency and utilization because it increases the capacity for lipid breakdown and absorption.

Signalling mechanism: Bile acids regulate the body's metabolism and nutrition absorption by acting as hormonal signals that activate particular receptors. The nuclear receptor known as Farnesoid X receptor (FXR) is directly activated by both free and conjugated bile acids; it is highly expressed in the kidney, intestines, and liver. Cholic acid (CA), lithocholic acid (LCA), deoxycholic acid (DCA), and chenodeoxycholic acid (CDCA) are the bile acid ligands that work the best with FXR (Wang et al., 2023; Yang et al., 2023). Hepatic glucose, cholesterol, and energy balance are all regulated by FXR activation (Chiang, 2013). Through mechanisms such as PPARa activation and the inhibition of lipogenesis, it regulates hepatic lipid metabolism. Additionally, it controls BA production by acting as a negative feedback loop, mainly by blocking the rate-limiting enzyme CYP7A1 through the intestinal FXR-FGF15/19 pathway and the liver's FXR-SHP (small heterodimer partner) axis (Wang et al., 2023; Li, et al., 2024a; Zheng et al., 2024). The gut microbiota and antibacterial defence are both regulated by FXR-induced antimicrobial peptides such iNOS and IL-18 (Li et al., 2024c).

The G protein-coupled membrane receptor (GPCR) TGR5 Receptor, which is also called Gpbar-1, is abundantly expressed in many different tissues and organs, including the gallbladder, intestine, spleen, skeletal muscle, kidney, adipocytes, pancreas, and macrophages (Chiang, 2013; Ding et al., 2020; Wang et al., 2023). Secondary bile acids (LCA and DCA) produced by the gut microbiota are the most powerful ligands for TGR5 (Wahlström et al., 2016; Wang et al., 2023). The signalling pathway, including TGR5, promotes the conversion of inactive thyroxine (T4) into active thyroid hormone (T3), which in turn increases energy expenditure, improves glucose tolerance, and increases insulin sensitivity (Chiang, 2013; Wahlström et al., 2016; Guo et al., 2020; Wang et al., 2023). Intestinal glucagon-like peptide-1 (GLP-1) release is enhanced by TGR5 activation, leading to increased insulin secretion. Protecting the intestines and liver from inflammation and steatosis, activating TGR5 also regulates immunological processes by reducing inflammation in macrophages (Swann et al., 2011; Halilbasic et al., 2013; Shapiro et al., 2018; Guo et al., 2020).

Gut microbiota regulation: There is a strong correlation between the composition of the gut microbiota and the metabolism and efficiency of BA. Microbes throughout the digestive tract undergo biotransformation processes on primary BAs, resulting in a wide variety of secondary BAs (such as DCA, LCA, and UDCA in humans), such as deconjugation, dehydroxylation, and epimerization. Because of these changes, the BA pool's signalling capabilities and hydrophobicity are altered (Wahlström et al., 2016; Jia et al., 2018; Bhusare et al., 2023; Li, et al., 2024c; Zheng et al., 2024). In addition to their indirect effect on the gut microbial population through activating FXR, which generates antimicrobial agents, BAs' detergent characteristics allow them to directly modulate the microbial community through breaking bacterial membranes (Chiang, 2013; Wahlström et al., 2016; Jia et al., 2018; Guo et al., 2020; Yin et al., 2021a; Ren et al., 2025). Bile acid-tolerant bacteria are encouraged to thrive by BAs, while bile acid-sensitive microorganisms are inhibited (Guo et al., 2020).

Effect of bile acids in freshwater aquaculture

The quest for alternatives to fish meal (FM) to mitigate feed expenses in intensive aquaculture has generated numerous research inquiries. Numerous studies have identified insect meals, mealworms, or plant protein sources as alternatives to fish meal. From an alternative viewpoint, the implementation of elevated carbohydrate and fat levels to diminish protein absorption by dietary additions such as bile acids has demonstrated efficacy. Prior research demonstrated that optimal supplementation of BAs can effectively improve productivity and liver health

while mitigating the adverse effects of plant protein sources when incorporated into meals (Yang et al., 2023; Li et al., 2024c; Zheng et al., 2024; Zhang et al., 2025). In freshwater aquaculture, exogenous bile acids (BAs) have been the subject of much research as a means to improve growth performance and general health by reducing metabolic stress brought on by less-than-ideal diets (those with a lot of carbohydrates or lipids). The fish species, BA type, and basal diet composition all have a significant impact on the effects and ideal BA inclusion levels. In Table 1 a brief summary has been depicted for easy understanding.

Table 1. Freshwater species-wise list of use and effects of bile acids

Sl	Species	Diet/Conditions	BA and dose	Results ↓ ↑	Reference
1.1	Nile tilapia (*Oreochromis niloticus*)	Isonitrogenous high fat diet (12% vs 6%), 60 days	Commercial bile acid; 150-200 mg/kg	Growth performance ↑, lipase and amylase ↑, GH, SOD, CAT, GPx ↑, Glucose, leptin, MDA ↓, intestinal and villi architecture ↑, Necrotic hepatocytes ↓	(Dawood et al., 2025)
1.2	Tilapia *(Oreochromis niloticus)*	Isonitrogenous, isolipidic diet (CP 32.1%, CL 7.6%) based on plant protein sorces; 63 days	Commercial BA; 200 mg/kg	FBW ↑, HSI ↑, VSI ↑, FCR ↓, TG ↓,	(Jiang et al., 2024)
1.3	Tilapia *(Oreochromis niloticus)*	Three hetero-nitrogenous (38-32% CP), hetero-lipidic (8-14% lipid) diet with three levels of bile acids; 60 days	Commercial BA; 500 mg/kg	Dietary BA reversed high lipid induced effects, WG SGR PER Lipase activity ↑, FCR SOD CAT GLU TAG ↓, best result with 35% CP, 11% lipid and 0.05% BA	(Bhusare et al., 2023)
1.4	Tilapia *(Oreochromis niloticus)*	Isonitrogenous and varying energy level diets containing different levels of CHO (40.1, 34.9, 29.9%) and lipids (6.1, 10.6, 16.1%); 56 days	Commercial BA (HDCA 69.9%, CDCA 18.9%, HCA 7.8%); 500 mg/kg	Optimum CHO:L (3.3:1) with BA increased final weight, TBG, SGR%, better immune response and health condition	(Elshenawy et al., 2020)
1.5	Tilapia *(Oreochromis niloticus)*	Vegetable protein-based diet (CP 32.3%, CL 5.7%); 63 days	Commercial BA (HCA 7.7%, HDCA 69.9%, CDCA 18.9%, others); 50-1350 mg/kg	Best weight gain at 150 mg/kg BA dose, Higher BA like 1350 mg/kg developed serious nuclear migration & vacuolation in hepatocytes	(Jiang et al., 2018)

Cont. Table 1.

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Sl	Species	Diet/Conditions	BA and dose	Results ↓ ↑	Reference
2.1	Grass carp (*Ctenopharyngodonidella*)	Low protein high lipid diet (26/6 vs 29/5), 50 days followed by 14 days challenge	Commercial BA (purity 98.2%); 165-211 mg/kg	Disease resistance and immunity ↑, Innate and adaptive immune function in SK, HK and SP ↑, Inhibit NF-κB signaling molecule, Activate TOR signaling molecule	(Zhao et al., 2025)
2.2	Common Carp (*Cyprinus carpio*)	Normal protein (32%) and high plant fat (10%) diet, 60 days	Commercial BA, Roneon (70%); 300 mg/kg	Growth indices ↑, Daily growth rate and condition factor ↑, Feed efficiency ↑	(Hekmatpoor et al., 2025)
2.3	Yellow River carp (*Cyprinus carpio*)	Isonitrogenous basal diet (CP 30.05; CL 5.96); 28 days	Liquid state BA (CDCA 5.74%, PCA 6.27%, CA 3.2%, HDCA 5.79%, HCA 2.31%); 10 ml/kg	Growth performance ↑, intestinal digestive ability ↑, antioxidant ability ↑, lipid deposition in liver ↓	(Zhao et al., 2024a)
2.4	Common carp (*Cyprinus carpio*)	High fat diet (CL 11% vs 5.4%), 56 days	Commercial BA (HCA 9%, HDCA 69%, CDCA 19%, others); 60 mg/kg	Addition of BA reversed the poor growth and increased serum TG due to high fat diet, BA reshaped good gut microbiota, upregulated PPARa	(Yang et al., 2023)
2.5	Common carp (*Cyprinus carpio*)	Isonitrogenous, isoenergetic plant protein-based diets; 77 days	Commercial BA (HCA 8%, HDCA 70.9%, CDCA 20.2%, others); 60 and 600 mg/kg	Growth performance ↑, intestine and hepatopancreas histopathology ↑, although 6o mg dose is recommended but 600 mg/kg dose was also reported beneficial and safe.	(Yao et al., 2021)
2.6	Grass carp (*Ctenopharyngodonidella*)	Low-protein and high-lipid diets (26% CP, 6% EE); 50 days.	Graded levels of BA; 0–320 mg/kg	Growth performance ↑, intestinal growth and function ↑, beneficial bacteria ↑, harmful bacteria ↓, immune function ↑	(Peng et al., 2019)
2.7	Grass carp (*Ctenopharyngodonidella*)	High lipid diet (7% vs 5%) with BA; 56 days	Commercial BA' 60 mg/kg	Lipid level in whole body, hepatopancreas and muscle ↓, Growth ↑, Lipid catabolism gene ↑, Amount of microbiota in intestine ↑	(Zhou et al., 2018a)

Cont. Table 1.

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Sl	Species	Diet/Conditions	BA and dose	Results ↓ ↑	Reference
3.1	Yellow catfish (*Pelteobagrus fulvidraco*)	Isonitrogenous high fat diet (15.96% vs 10.58%), 70 days	Chenodeoxycholic acid, CDCA (98% purity); 900 mg/kg	High fat induced growth retardation, lipid accumulation and BA metabolism disorder ↑	(Zheng et al., 2024)
3.2	Yellow catfish (*Pelteobagrus fulvidraco*)	High fat diet (15.96% lipid vs 10.58%); 50 days	Chenodeoxycholic acid, CDCA (98% purity); 900 mg/kg	BA attenuated the increased abundances of mRNA of seven lipid metabolic genes observed in different organs	(Li et al., 2024b)
3.3	Striped catfish (*Pangasianodo-nhypophthalmus*)	Isonitrogenous, isolipidic diet (CP 31.7%, CL 5.2%), 70 days	Commercial BA (HCA 6.2%, HDCA 53.1%, CDCA 13.7%, others); 1000-1250 mg/kg	Growth, nutrient utilization & immunity ↑, expression of ATGL, HSL & CPT-1 ↑, PPARa and FAS ↓	(Adam et al., 2023)
4.1	Spotted seabass (*Lateolabrax maculatus*)	Isonitrogenous, isolipidic diet (CP 43%, CL 12%) 56 days	Commercial BA (HDCA 75.2%, CDCA 17.4%, HCA 4.2%); 800 mg/kg	WG% ↑, FCR ↓, Enzyme activity and transcripts of gluconeogenesis in liver ↑, Lipase activity ↑, intestinal intestinal antioxidant capacity ↑, intestinal inflammatory response inhibited	(Liu et al., 2024)
4.2	Largemouth bass (*Micropterus salmoides*)	Isonitrogenous, isolipidic diet (CP 50.4%, CL 12%) with positive control 5% á starch and negative control 10% á starch; 56 days	Commercial BA (HCA 8.0%, HDCA 70.9%, CDCA 20.2%); 200-1000 mg/kg	Carbohydrate utilization ↑, antioxidant capacity ↑, intestinal microbiota and inflammation ↑	(Li et al., 2024c)
4.3	Large mouth sea bass (*Micropterus salmoides*)	Isonitrogenous, isolipidic diet (CP 46%, CL 10%), 56 days	Commercial BA; 300 mg/kg	Growth performance ↑, Serum GLU TG TC AL T AST MDA ↓, SOD CAT GSH-Px ↑, liver & intestinal antioxidant capacity ↑,	(Jia et al., 2024)
4.4	Large mouth sea bass (*Micropterus salmoides*)	Isonitrogenous diets (8) with graded level of fat (9-12%) and starch; 56 days	Ox bile; 1000 mg/kg	Highest weight gain in low fat high starch with BA group, BA partially mitigated hepatic injuries	(Romano et al., 2022)
4.5	Large mouth sea bass (*Micropterus salmoides*)	Isonitrogenous, high lipid diet (CP 49%, CL 18 vs 10%), 63 days	CDCA; 300-900 mg/kg	No significant difference in growth performance, digestion and absorption of lipid ↑, antioxidant capacity and intestinal health ↑	(Yin et al., 2021b)

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Table 1., Cont. ...

Sl	Species	Diet/Conditions	BA and dose	Results ↓ ↑	Reference
4.6	Large mouth sea bass (*Micropterus salmoides*)	Isonitrogenous diets with high starch (19%); 56 days	Bile acid; 350 mg/kg	WG and PER ↑ in BA group, SOD and CAT ↑, MDA ↓, ALT AST ALP GLU ↓, TG TC ↑, plasma immunoglobulin and lysozyme activity ↑, improved liver histopathology	(Guo et al., 2020)
5.1	Rice field eel (*Monopterus albus*)	Isonitrogenous basal diet (CP 42.6; CL 7.9); 56 days	Commercial BA, purity 95% (HDCA+CA 77%, CDCA 17%); 250 mg/kg	Growth performance ↑, antioxidant capacity of liver and intestine ↑, lipid deposition in liver ↓, Higher dose of BA cause vacuolation and rupture of hepatocytes,	(Wei et al., 2024)
5.2	Rice field eel (*Monopterus albus*)	High fat diet (CL 13% vs 7%), 56 days	Commercial BA (HDCA+HCA e" 77%; CDCA e" 17%, others); 250 mg/kg	Weight gain ↑, SGR ↑, FCR ↓, lipid deposition in liver, muscle & whole body ↓, intestinal structural integrity ↑, intestinal health ↑	(Lei et al., 2023)
6.1	Allodiploid hybrid fish derived from blunt snout bream (♀) × topmouthculter (♂)	Basal diet and duckweed powder to make herbivorous diet, 56 days	Cholic acid; 600 mg/kg	Growth performance ↑, Intestinal digestive ability ↑, Adaptation to herbivorous diet ↑, Gene expression related to intestinal growth-digestion-absorption ↑, Gut probiotics ↑, Gut pathogenic flora ↓	(Zhou et al., 2025)

BA- Bile acid; CA- Cholic acid; HCA- Hyocholic acid; HDCA- Hyodeoxycholic acid; CDCA- Chenodeoxycholic acid; ↓- Decrease; ↑- Increase; GH- Growth hormone; SOD- Superoxide dismutase; CAT- Catalase; GPx- Glutathione peroxidase; MDA- Malondialdehyde; FBW- Final body weight; HIS- Hepatosomatic index; VSI- Viscerosomatic index; FCR- Feed conversion ratio; TG- Triglyceride; WG- Weight gain; SGR- Specific growth rate; PER- Protein efficiency ratio; GLU- Glucose; TAG- Triacylglycerol; TBG- Total body gain; CHO:L- Carbohydrate to lipid; SK- Skin; HK- Head-kidney; SP- Spleen; TOR- Target of rapamycin; NF-κB- Necrosis factor-κB; ATGL- Adipose triglyceride lipase; HSL- ,Hormone-sensitive lipase; PPARα-Peroxisome proliferator-activated receptor α; CPT-1- Carnitine palmitoyl transferase 1; FAS- Fatty acid synthase; TC- Cholesterol; ALT- Alanine aminotransferase; AST- Aspartate aminotransferase

Effect on growth: Dietary BA supplementation generally results in a substantial rise in growth metrics and nutrient utilization parameters such as final body weight (FBW), weight gain rate (WGR), and specific growth rate (SGR), alongside a notable reduction in the feed conversion ratio (FCR) and an enhancement in protein efficiency ratio (PER) (Bhusare et al., 2023; Adam et al., 2023; Lei et al., 2023; Jiang et al., 2024; Hekmatpoor et al., 2025). Using BAs had a good influence on growth performance in multiple investigations, including diverse species. A number of bile acid functions, such as improving lipid utilization, controlling energy metabolism, and influencing the immune and antioxidant systems, may contribute to their growth-promoting effect (Bhusare et al., 2024). Researchers found no evidence of growth retardation

in juvenile largemouth bass (*Micropterus salmoides*) when given a high-starch diet that also contained bile acid (Guo et al., 2020). At least four variables, including fish species, dietary bile acid level, bile acid kinds, and basal diet composition, are associated with the growth-promoting effects of bile acid, (Wang et al., 2023). Because many fish species have varied dietary lipid levels, bile acid requirements and tolerances also vary by species also. In general, carnivore species require higher levels as because of higher dietary lipid requirement. The growth performance of black sea bream was found to be lowered at a dosage of 200 mg/kg, according to Jin et al. (2019), whereas a dosage of 1000 mg/kg bile was shown to boost growth in snakehead (*Channa argus*) according to Hou et al. (2019). According to research on tilapia (*Orechromis niloticus*), the appropriate amount of bile acids promotes growth, but beyond a certain point, growth performance becomes impaired. Dietary bile acid levels enhanced growth performance steadily from 0 to 150 mg/kg, but dropped dramatically between 450 mg/kg and 1350 mg/kg, suggesting optimum level as 150 mg/kg (Jiang et al., 2018). According to Peng et al. (2019), a high dose of 320 mg/kg of bile acid inhibited growth in grass carp (*Ctenopharyngodon idella*), while the optimal dose of 170 mg/kg resulted in improved growth. Varieties of bile acids also contribute to different levels of growth performance. According to several studies (Du et al., 2018; Xiong et al., 2018; Kong et al., 2022), certain fish have chenodeoxycholic acid (CDCA) as their primary bile acid and lithocholic acid (LCA) as their secondary bile acid. Primary bile acids, such CDCA, or commercial bile acids usually have no effect on growth or a positive effect. But secondary bile acids (such LCA) caused cholestasis and liver injury, which could hinder the fish's development. There are a number of possible mechanisms via which the composition of the basal diet, especially the amount of lipids or carbohydrates, influences bile acid activity. Overall improvement in different growth metrics was contributed by efficient nutrient utilization. BAs being powerful physiological detergents and signalling molecules, regulate digestion, absorption, transport and metabolism of major nutrients, particularly lipids and carbohydrates (Wang et al., 2023; Yang et al., 2023). BAs have influential role in regulating gut microbiota towards better nutrient utilization (Li et al., 2024a).

Digestive process: Using bile acid as an addition protects the gall bladder and liver and also stimulates hepatocytes to secrete bile through the action of its components (Gu et al., 2017; Elshenawy et al., 2020). In the gastrointestinal tract, bile acids play an essential role in fat digestion by increasing the lipase enzyme's activity and making lipids more soluble. Digestion, absorption of fat-soluble vitamins, and gut microbiota structure are all significantly impacted by BAs. *Oncorhynchus mykiss*, a species of rainbow trout, showed enhanced feed utilization when BAs were added to a diet mainly formulated with of plant protein sources (Adhami et al., 2017). Similarly, when rainbow trout were administered BAs in conjunction with standard diets primarily composed of soybean meal, there was an enhancement in growth and feed efficiency (Staessen et al., 2020). In addition, the ingestion of dietary bile acids (BAs) has been shown to improve the growth, body composition, lipid digestion, and microbiota in various fish species, such as grass carp (*Ctenopharyngodonidella*) (Zhou, et al., 2018a), Japanese flounder (*Paralichthys olivaceus*) (Alam et al., 2001), juvenile black seabream (*Acanthopagrus schlegelii*) (Jin et al., 2019), tongue sole (Li et al., 2021), and Nile tilapia (*Oreochromis niloticus*) (Jiang et al., 2018; Elshenawy et al., 2020). Bile salts facilitate lipid digestion by emulsifying lipids into minute chylous particles, hence enhancing the interaction between lipase and lipids to catalyse the hydrolysis of ester bonds (Ding et al., 2020; Romano et al., 2020).

Liver function: In fish, the gut is of critical importance to the absorption of nutrients and to the regulation of immune function. The negative impact of a diet that is high in fats and carbohydrates on the anatomy and function of the intestines in a variety of fish species has been thoroughly shown in multiple studies (Yu et al., 2020; Wang et al., 2022). When it comes to generating energy, using lipids or carbohydrates at a higher level to substitute a portion of protein has detrimental effects, primarily on the liver. BAs, play a role as direct metabolic signals in the liver. It has been proven that these acids stimulate the proliferation of liver cells, which in turn reduces the amount of damage, including inflammation and oxidative stress. During the process of liver regeneration, the activation of liver cell receptors is an important factor (Romano et al., 2022). Farmers occasionally report that the livers of certain farmed fish, such as Magur, exhibit colour deviation. It is possible that there is a connection between this phenomenon and higher dietary fat or carbohydrates, although this has not been definitively established. Research seems to indicate that a diet that is strong in starch is the reason for the shift in hue

(Lin et al., 2018; Guo et al., 2020). Histopathological assessment, particularly of the liver and intestine sections, gave clear indications of the effects of bile acid against a high-fat or high-starch diet (Lei et al., 2023).

Lipid and carbohydrate metabolism: Previously, the main functions of bile acids were considered to be of emulsification of fat to facilitate digestion and absorption. Since the discovery of Farnesoid X receptor (FXR) and other natural ligands more studies focused to asses bile salt as a signal molecule for fat metabolism (Zhang et al., 2022). Dietary bile acid increases the expression of *fxr* in the liver, which can induce the upregulation of the gene like *ppar* to enhance oxidation of fatty acids (Pineda Torra et al., 2003). High fat, diets often promote fatty liver. Bile acid that is consumed through diet plays a beneficial role in reducing the amount of lipid accumulation. The appropriate digestion of the lipid while it is in the presence of dietary bile acids is what causes this action to be exerted, which allows for the utilization of the extra lipids. Several studies are conclusive about the said role in different fish species like, grass carp (Zhou et al., 2018a), common carp (Yao et al., 2021), large- mouth bass (Yin et al., 2021b), black sea bream (Jin et al., 2019), and large yellow croaker (Du et al., 2018). Farnesoid X receptor (FXR) and Takeda G protein-coupled receptor 5 (TGR5) are the two main targets for control of bile acid synthesis, transport, and reabsorption. Bile acids serve as key molecular signals in intestinal and liver metabolism pathways, acting through receptors like TGR5 and FXR to regulate lipid and glucose metabolism (Chiang, 2013). Research on fish has demonstrated that manipulating FXR not only maintains bile acid balance but also influences lipid and glucose metabolism positively (Schonewille et al., 2016). FXR can be activated by specific bile acids, with CDCA being the most potent activator followed by CA, DCA, and LCA. Primary bile acids exhibit stronger FXR agonistic effects compared to secondary bile acids. Additionally, taurine-conjugated primary bile acids such as UDCA, α, and β muricholic acid (TáMCA, TâMCA) act as FXR antagonists in rodents (Wahlström et al., 2016, 2017). Other genes like *srebp1, atgl, hsl, ppar, cpt1, fas* etc. are also indicative of effect of bile acid on lipid metabolism (Issemann & Green, 1990; Ruiz et al., 2014; Adam et al., 2023; Zhao et al., 2024b).

The activation of the FXR-FGFR4-CYP7A1 pathway, according to research, resulted in the regulation of liver bile acid production and metabolism in largemouth bass when bile acid supplements were administered. During this time, the expression of *foxo1* and other genes that are connected to the process of gluconeogenesis, such as *g6pc, fbp1,* and *gs*, was suppressed by the presence of bile acids, while the expression of genes that are related to the process of glycolysis, such as *pfkl* and *gk*, was enhanced. This enhancement was accomplished by activating the insulin pathway. In addition, the diversity of gut microbiota was boosted by a diet high in carbohydrates along with bile acid supplementation. This diet also modified the relative abundance of certain phyla and genera that are associated with carbohydrate metabolism and energy balance, and it improved the inflammatory response of the intestines. Those findings showed that the incorporation of dietary bile acids in the diets of largemouth bass resulted in improvements in carbohydrate utilization, antioxidant capacity, and intestinal microbiota, as well as a reduction in inflammation (Wang et al., 2023; Yang et al., 2023; Li et al., 2024c).

Health and immunity: Supplementing freshwater fish with BA has a significant positive impact on their health by strengthening their defence mechanisms. BA markedly enhances antioxidant levels (Wang et al., 2023). This is evidenced by a notable reduction in hepatic malondialdehyde (MDA) levels, a biomarker for lipid peroxidation and oxidative stress, alongside a substantial enhancement in the activity of antioxidant enzymes such as hepatic catalase (CAT), superoxide dismutase (SOD), and total antioxidant capacity (T-AOC) in species including thinlip mullet, largemouth bass, and tilapia (Guo et al., 2020; Yin et al., 2021b; Adam et al., 2023; Bhusare et al., 2023; Liu et al., 2026). Dietary BA enhances serum immunity. Serum lysozyme levels, respiratory burst activity, alternative complement activities, and immunoglobulin concentrations were markedly elevated in thinlip mullet and largemouth bass (Guo et al., 2020; Abdel-Tawwab et al., 2023; Li et al., 2024a). BA supplementation markedly reduced liver function enzymes, including aspartate aminotransferase (AST) and alanine aminotransferase (ALT), in thin lip mullet, signifying diminished hepatocyte injury. BA shown efficacy in mitigating hepatic fibrosis in *M. salmoides* produced by a high-starch diet (Lei et al., 2023; Wang et al., 2023; Li et al., 2024c). BA supplementation can enhance intestine structural integrity (e.g., elevated intestinal fold height in largemouth bass) and mitigate intestinal inflammatory reactions. The introduction of BA modified the

intestinal microbiota in largemouth bass, altering the relative abundance of genera associated with glucose metabolism and energy homeostasis, while enhancing the intestinal inflammatory response by diminishing pro-inflammatory gene expression. In grass carp, BA supplementation modified the gut microbiota, reducing detrimental bacteria such as *Escherichia coli* and *Aeromonas*, while enhancing good bacteria like *Bifidobacterium* and *Lactobacillus* (Li et al., 2024c).

Challenges and future scopes

Although research has clarified that optimal supplementation of BAs can effectively improve productivity and liver health (Zhou et al., 2018b; Ding et al., 2020; Yin et al., 2021b), while mitigating the adverse effects of plant protein sources when incorporated into diets (Jiang et al., 2018), there are still many challenges related to toxicity, dosage and species variability for successful implementation of bile acids as additives. High levels of BAs have the potential to be cytotoxic (Amirkolaei et al., 2025). The administration of an overdose (1350 mg of BAs per kilogram of food) to tilapia (*O. niloticus*) caused decreased liver function as well as severe nuclear migration and vacuolization in hepatocytes (Jiang et al., 2018; Wang et al., 2023). Nuclear migration and vacuolization inside hepatocytes were observed in striped catfish (*P. hypophthalmus*) when they had high levels (1500 mg/kg) of the substance in their systems (Adam et al., 2023). Genetically enhanced farmed tilapia have their growth performance drastically reduced by overdosed BAs (1350 mg/kg) (Jiang et al., 2018). In addition, grass carp (*C. idella*) had stunted development and impaired intestinal immunity when exposed to levels as high as 320 mg/kg (Peng et al., 2019). The trophic level and dietary lipid needs of the fish determine the appropriate BA inclusion level, which is species dependent. For example, according to meta-regression analysis (Li et al., 2024a), the ideal range for medium-trophic-level freshwater fish (such as tilapia or largemouth bass) was determined to be 989.42 mg/kg, but the optimal range for low-trophic-level fish (such as grass carp) was 60-188.42 mg/kg. Further, different basal diets have different effects on the efficacy of BA supplementation. In GIFT tilapia that was fed a diet with low protein (32% CP) and extremely high lipid (14%), growth retardation caused by "high lipid mediated excessive stress" was evident (Bhusare et al., 2023). Supplemental BA could ameliorate hepatic difficulties in certain carnivorous freshwater species, such as largemouth bass (*M. salmoides*), which were negatively affected by high-carbohydrate diets (Li et al., 2024c). Different BA types (e.g., primary vs. secondary) also have varying regulatory effects on metabolism, antioxidants, and the immune system, resulting in different outcomes on growth (Du et al., 2018; Xiong et al., 2019; Kong et al., 2021). More research on the molecular pathways is needed to completely understand the involvement of exogenous BAs in lipid metabolism. Many commercial BA products utilized in research contain complex bile acid profiles, making it difficult to determine the independent effect of each individual BA type. Little is known about the precise immunomodulatory mechanisms of dietary exogenous BAs in fish, highlighting the need for further investigation. Future research should continue to investigate and define the best dietary BA inclusion levels for different freshwater fish species, taking into account changes in basal diet compositions, dietary lipid and cholesterol content, and life stage. Examining the individual impact of specific bile acid types (e.g., chenodeoxycholic acid (CDCA), hyodeoxycholic acid (HDCA), taurocholic acid (TCA) can facilitate the identification of the most efficient and cost-effective bile acid combinations for commercial feed use. Modulating the intestinal microbiota to modify the bile acid pool (e.g., by affecting bile salt hydrolase activity) is suggested as a safer and potentially more effective alternative to direct administration of exogenous bile acids. Hence, bacteria that produce bile salt hydrolase (BSH) isolated from fish intestines may be employed as probiotics in aquafeed.

Conclusion

Due to function in enhancing nutrient utilization and alleviating metabolic stress, exogenous bile acids (BAs) have established themselves as attractive functional feed additives in freshwater fish farming. Overall, BAs improve growth performance, which includes feed conversion ratio (FCR), final body weight (FBW), and specific growth rate (SGR). Particularly when fish are fed diets rich in lipids or plant-based proteins, they help reduce harmful health effects such liver damage, hepatic lipid accumulation, and elevated levels of circulating triglycerides and total cholesterol. Yet, dose-dependent toxicity poses a problem for the application. When given in excess, BAs can stunt development, affect liver function (including vacuolization and nuclear migration), and even cause severe fatalities. The mix of the basal diet and the species involved must be carefully considered when formulating the optimal inclusion levels. Determining these ideal, non-toxic doses and investigating the

impacts of specific BA chemicals should be the priorities of future work to fully explore potentiality of BA in freshwater aquaculture.

Conflict of interest: The Authors have no conflicts of interest in this study.

Author's contribution: SD: Conceptualization, Writing, data curation; IK: Editing and reviewing; AM: Editing and reviewing; PNC: Editing and reviewing; GPM: Conceptualization, editing, supervision.

Data availability statement: The data set generated during research needs to be available from the corresponding author upon reasonable request.

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