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Dietary *Lycium barbarum* polysaccharide modulates growth performance, antioxidant capacity, and glucolipid metabolism in largemouth bass (*Micropterus salmoides*) fed with high- carbohydrate diet

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To investigate the ameliorative effects of *Lycium barbarum* polysaccharide (LBP) on growth performance, oxidative stress, and glucolipid metabolism in largemouth bass (*Micropterus salmoides*) fed with high-carbohydrate diets. Fish (41.81 ± 0.36) g were fed on high-carbohydrate diets (15% α-starch) supplemented with 0% (15% α-Starch and no LBP, HLBP), 0.2g/kg LBP (LBPO.2), 0.4g/kg LBP (LBPO.4), 0.6g/kg LBP (LBPO.6) and 0.8g/kg LBP (LBPO.8) for 56 days. An additional low-carbohydrate (10% α-starch) dietary group (10% α-Starch and no LBP, NLBP) was set up and fed for the same 56 days. The final body weight (FBW), weight gain ratio (WGR), and specific growth rate (SGR) of fish in the LBPO.6 group were the highest, and the treatment groups were all significantly higher than in the HLBP group ($P < 0.05$). The activities of AMS, LPS, and TPS in the intestine and liver were all highest in the LBPO.6 group and significantly higher than in the HLBP group ($P < 0.05$). In the intestine and liver, the activities of T-AOC, CAT, GSH-PX, and SOD were significantly higher in the LBPO.6 and LBPO.8 groups than in the HLBP group ($P < 0.05$). The expression of *CAT*, *SOD*, and *GPX* genes were highest in the LBPO.8 group and significantly higher than in the HLBP group ($P < 0.05$). In the intestine and liver, the expression of *IL-1β*, *IL-8*, and *TNF-α* genes were significantly lower in the LBPO.4, LBPO.6, and LBPO.8 groups than in the HLBP group ($P < 0.05$); the expression of *IL-10* and *TGF-β1* genes were significantly higher in the LBPO.6 and LBPO.8 groups than in the HLBP group ($P < 0.05$). The expression of *GK*, *PFK*, and *G6P* genes were significantly higher in the LBPO.6 and LBPO.8 groups than in the HLBP group ($P <$

0.05). The expression of *ACC*, *CPT-1*, and *FAS* genes were significantly higher in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$). In summary, the addition of 0.6 g/kg LBP was effective in ameliorating the negative effects of a high-carbohydrate diet on largemouth bass.

KEYWORDS

Lycium barbarum polysaccharide, largemouth bass (*Micropterus salmoides*), growth performance, antioxidant capacity, inflammation response, glucolipid metabolism

1 Introduction

Fish require protein as a necessary macronutrient to sustain their regular lifestyle. In aquatic feed, protein is the most expensive macronutrient (Wang et al., 2023). In actual production, the cheapest carbohydrate is frequently employed to promote protein-sparing action and improve feed physical qualities in order to lower feed costs (Li et al., 2020a). However, fish's capacity to digest and metabolize carbohydrates is restricted, and the utilization efficiency of dietary carbohydrates varied among different fish species (Kamalam et al., 2012). Therefore, a diet high in carbohydrates may be harmful to fish health (Wang et al., 2022a). It has been reported that supplementing diets with 20% dietary starch can negatively affect largemouth bass (Lin et al., 2018; Zhang Y. et al., 2020; Romano et al., 2022). It has also been reported that the addition of 15% dietary carbohydrates resulted in the accumulation of glycogen and liver lipids in largemouth bass (Ma et al., 2019). As a result, there is increasing interest in ways to mitigate the negative effects of high-carbohydrate diets on carnivorous fish.

Studies have reported that adding plant extracts to high-carbohydrate diets can improve growth, immunity, and hepatic glucolipid metabolism in fish (Wang et al., 2024). Additionally, numerous plant extracts are known to promote growth, enhance immunity, and combat pathogens in aquaculture (Liu et al., 2023). *Lycium barbarum* is a plant in the Solanaceae family that is widely distributed in northwestern China. It has also been imported to North and South America as well as Western Europe (Liu H. et al., 2022). Because *Lycium barbarum* is rich in nutrients and active components such as amino acids, polysaccharides, polyphenols, vitamins, and trace elements, it is used as a frequent tonic and in traditional Chinese medicine in China (Amagase and Farnsworth, 2011; Liu et al., 2024). More than 200 different components have been identified, characterized, and analyzed to date. Polysaccharides, vitamins, betaine, and mixed extracts from goji berries are considered beneficial to health, offering anti-aging properties, improved vision, and fatigue resistance (Yao et al., 2018). *Lycium barbarum* polysaccharide (LBP), a water-soluble polysaccharide extracted from *Lycium barbarum*, is primarily

composed of various monosaccharides, including arabinose, galactose, glucose, mannose, rhamnose, and xylose (Wu et al., 2010), and has been identified as one of the active ingredients responsible for biological activities (Shan et al., 2011). Previous studies have shown that LBP has antioxidant (Jin et al., 2013), immunomodulatory (Zhang et al., 2011), hypoglycemic (Tang et al., 2015), and anti-inflammatory (Tian et al., 2019). *Lycium barbarum* polysaccharides, as immunomodulatory agents, can enhance the immune defense capabilities of fish, thereby increasing their resistance to pathogens and reducing the incidence of diseases (Tan et al., 2019a). The regulation of carbohydrate and lipid metabolism is crucial for maintaining energy balance and preventing metabolic-related diseases. LBP can modulate these processes by influencing key enzymes involved in carbohydrate and lipid metabolism, thereby helping to maintain normal physiological functions and enhance growth performance (Jia et al., 2024). Furthermore, studies have shown that LBP may reduce liver injury and oxidative stress in the organism caused by lipid deposition (Li et al., 2007; Wu et al., 2024). The antioxidative capacity is particularly important for neutralizing oxidative stress induced by high-carbohydrate diets. Oxidative stress is a key factor leading to cellular damage and aging. The antioxidative components in LBP can effectively scavenge free radicals and mitigate inflammatory responses, thereby protecting cells from damage (Tian et al., 2019). Therefore, we speculated that LBP could mitigate the damage of high carbohydrate diets on fish organisms.

The largemouth bass (*Micropterus salmoides*), originally from the United States, was introduced into China in the 20th century (Yang et al., 2023). Its production has reached 0.7 million tons due to its rapid growth, high quality meat, high yields and strong adaptability in China (Li et al., 2020b; Zhou et al., 2022). The consumer market for largemouth bass has great potential in China (Lin et al., 2020). However, under the current intensive farming conditions, high-carbohydrate diets burden the growth performance and organismal health of largemouth bass. Therefore, we chose LBP as a functional additive to explore its ability to alleviate the negative effects of high-carbohydrate diets on largemouth bass.

2 Materials and methods

2.1 Experimental animals and diet preparation

Healthy fish and base feed were supplied by Zhejiang Huzhou Hai Huang Biotechnology Co. (Huzhou, China). The fish were given a 7-day acclimatization period before the experiment to become used to the environment and amenities. The initial weight of the fish was (41.81 ± 0.36) g. The feed composition of each experimental group is shown in Table 1. The experimental groupings are as follows: 10% α -Starch and no LBP(NLBP); 15% α -Starch and no LBP(HLBP); 15% α -Starch and 0.2% LBP(LBP0.2); 15% α -Starch

and 0.4% LBP(LBP0.4); 15% α -Starch and 0.6% LBP(LBP0.6); 15% α -Starch and 0.8% LBP(LBP0.8).

2.2 Feeding trial

The trial was carried out in an indoor system. After acclimatization and being fasted for 24 h, fish were randomly distributed into 18 cement tanks (1.50 m \times 1.50 m \times 1.0 m, the height of water 0.8 m). These tanks were randomly divided into six treatments with three replicates each, with 30 fish for each tank. During the eight weeks of feeding trial, fish were fed two times per day at 7:00 and 16:00, the feeding rate was 5% of body weight. Two-third of the water in each

TABLE 1 Formulation of the diet (% dry weight).

Ingredients	NLBP	HLBP	LBPO.2	LBPO.4	LBPO.6	LBPO.8
White fish meal	45	45	45	45	45	45
Soybean protein concentrate	5	5	5	5	5	5
Soybean meal	2	2	2	2	2	2
Squid paste	4	4	4	4	4	4
Yeast	1	1	1	1	1	1
Corn powder	3	3	3	3	3	3
Brewer's yeast	4	4	4	4	4	4
Corn protein powder	3.5	3.5	3.5	3.5	3.5	3.5
Dried blood	4	4	4	4	4	4
Soybean phospholipid oil	1	1	1	1	1	1
Soybean oil	4.5	4.5	4.5	4.5	4.5	4.5
microcrystalline cellulose	6	1	0.8	0.6	0.4	0.2
α -Starch	10	15	15	15	15	15
Fish oil	2.5	2.5	2.5	2.5	2.5	2.5
<i>Lycium barbarum</i> polysaccharides	0	0	0.2	0.4	0.6	0.8
Calcium biphosphate	1	1	1	1	1	1
Choline chloride	0.5	0.5	0.5	0.5	0.5	0.5
Vitamins premix ^a	1.5	1.5	1.5	1.5	1.5	1.5
Minerals premix ^b	1.5	1.5	1.5	1.5	1.5	1.5
Total	100	100	100	100	100	100
Nutrient levels (%)						
Crude protein	46.19	46.58	46.63	46.31	46.84	46.72
Crude lipid	12.58	12.83	12.75	12.88	12.65	12.81
Crude Fiber	8.13	2.51	2.38	2.11	1.91	1.78
Nitrogen-Free Extrac	16.82	20.85	20.87	21.07	21.05	20.89
Energy (MJ/kg)	19.61	19.56	19.53	19.64	19.71	19.44

^aVitamins premix (IU or mg/kg dry diet). vitamin A, 40000 IU; vitamin D, 10000 IU; vitamin E, 250; vitamin K, 50; vitamin B1, 75; vitamin B2, 75; vitamin B6, 40; vitamin B12, 0.1; niacinamide, 200; calcium-D-pantothenate, 125; folic acid, 12.5; biotin, 0.4; inositol, 500.

^bMinerals premix (mg/kg dry diet). Ca, 52.5; K, 450; Mg, 60; Fe, 5; Cu, 15; Zn, 50; Mn, 19; Co, 4; Se, 0.1.

tank was renewed twice a week. During the feeding trial, the temperature in the water was (28 ± 0.5) °C; dissolved oxygen was at least 6.0 mg/L; pH was 7.5–8.3, and nitrate level was under 0.03 mg/L.

2.3 Sample collection

At the end of the feeding trial, the fish were fasted for 24 h. Fish in each tank were weighted and counted individually. Blood was collected from the tail vein (1 mL), and centrifuged (4°C, 1600×g for 10 min) after preserved in 24°C for 4 hours. The serum was collected and stored at –20°C. The intestine and liver of fifteen fish per treatment (five fish per tank) were dissected using sterilized surgical tweezers and scissors, then immediately frozen in liquid nitrogen and stored at refrigerated (–80°C) until further analysis was conducted. All experimental fish were anaesthetized with tricaine methanesulfonate (MS-222) before collecting the samples. The general culturing and sampling of experimental fish were in accordance with Shanghai Ocean University’s ethical guidelines for the care and use of laboratory animals.

2.4 Biochemical indices for serum

Serum biochemical indices was determined as follows: triglyceride (TG), total cholesterol (TC), high-density lipoprotein (HDL), low-density lipoprotein (LDL), alanine (ALT) and aspartate transaminase (AST), alkaline phosphatase (AKP) activities were quantified in the serum. The test kits are provided by Nanjing Jiancheng Bioengineering Institute (Nanjing, China).

2.5 Digestive enzyme activity

Digestive enzyme activity was determined as follows: Amylase (AMS), Lipase (LPS), and Trypsin (TPS) activities were quantified in the intestinal and liver of fish by the commercial detection kits of Nanjing Jiancheng Bioengineering Institute (Nanjing, China) according to the manufacturer.

2.6 Antioxidant enzyme activity

Antioxidant capacity was determinate as follows: total antioxidant capacity (T-AOC), catalase (CAT), glutathione peroxidase (GSH-PX), superoxide dismutase (SOD) activities, and malondialdehyde (MDA) content were quantified in the intestinal and liver of fish by the commercial detection kits of Nanjing Jiancheng Bioengineering Institute (Nanjing, China) according to the manufacturer.

2.7 Gene expression analysis

According to the manufacturer’s instructions (Takara, China), total RNA was isolated from intestinal and liver by using Trizol reagent. (Takara, China). Nanodrop 2000 (Thermo Scientific, USA) was used to quantitate the concentration of RNA. The obtained RNA samples were reversely transcribed to cDNA by NovoScript® Plus All-in-one 1st Strand cDNA Synthesis SuperMix. (Novoprotein, China). Real-time quantitative RT-qPCR was performed on LightCycler (Roche, China). All RT-qPCR primers were designed by the Primer 5 software. The primers for these genes

TABLE 2 Sequences of the primers used in real-time qPCR.

Gene	Forward (5' – 3')	Reverse (5' – 3')	Reference
CAT	TGCTGTCCGCTTCTCCAC	TCCCAGTTGCCCTCCTCA	XM_038704976.1
SOD	AGACAATACAAATGGGTGC	CTTTGCGACATTATCTGCT	XM_038708943.1
GPX	GGGACTCGTTATCTGGG	AGGAGCTGGAAGTTTGGT	XM_038697220.1
IL-1β	CGTGACTGACAGCAAAAAGAGG	GATGCCAGAGCCACAGTTC	XM_046034892.1
IL -8	CGTTGAACAGACTGGGAGAGATG	AGTGGGATGGCTTCATTATCTTGT	XM_038704089.1
TNF-α	CTTCGTCTACAGCCAGGCATCG	TTTGGCACACCGACCTCACC	XM_046046126.1
IL-10	CGGCACAGAAATCCAGAGC	AGCAGGCTCACAAAATAACATCT	XM_038696252.1
TGF-β1	GCTCAAAGAGAGCGAGGATG	TCCTCTACCATTGCAATCC	XM_046074257.1
GK	AAAAGGAGGGAGAACGGGTA	AGAGCGAGCAACACAAGGAT	XM_038720816.1
PFK	GGGTGTGGAGATGACGAAGT	GGGTGTGGAGATGACGAAGT	XM_038720351.1
G6P	GGGAGACCAGGTGTGTGTCT	GGTAGAAGCCAACAGCGAAG	XM_038735542.1
ACC	CAGGTCAGTGGAGCTGTCAA	CAGGTCAGTGGAGCTGTCAA	XM_038709726.1
CPT-1	AACGGATGGAGGCTTTGACC	CTACACCTGGGACACGACTG	XM_038695351.1
FAS	CAACAAGCTGCCTACGATGA	CAACAAGCTGCCTACGATGA	XM_038735140.1
β-actin	TTCACCACCACAGCCGAAAG	TCTGGGCAACGGAACTCT	XM_038695351.1

are listed in Table 2. The $2^{-\Delta\Delta Ct}$ comparative CT method was employed to quantitate expression levels for *CAT*, *SOD*, *GPX*, *IL-1 β* , *IL-8*, *TNF- α* , *IL-10*, *TGF- β 1*, *GK*, *PFK*, *G6P*, *ACC*, *CPT-1*, and *FAS* genes relative to the β -actin gene.

2.8 Calculations and statistical analysis

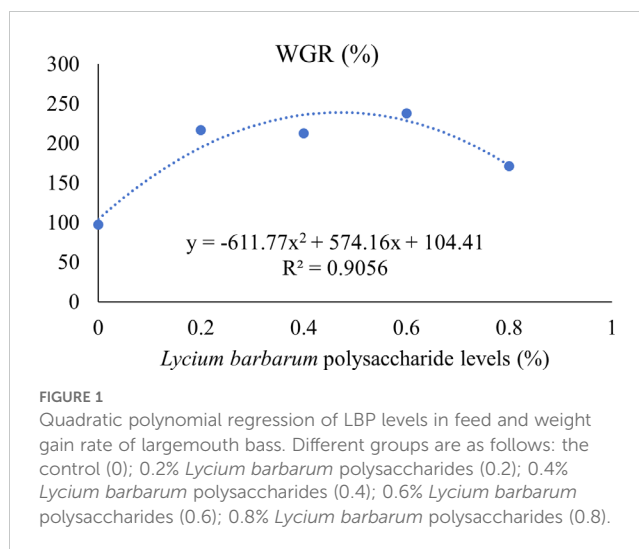
- Calculation formula of growth indexes:
 - Weight gain rate (WGR, %) = $100 \times (\text{final weight} - \text{initial weight})/\text{initial weight}$
 - Specific growth rate (SGR, %/day) = $100 \times [\ln(\text{final weight (g)}) - \ln(\text{initial weight (g)})]/\text{days}$
 - Hepatosomatic index (HSI, %) = $100 \times [\text{liver weight (g)}/\text{body weight (g)}]$
 - Survival rate (SR, %) = $100 \times (\text{number of final fish}/\text{numbers of initial fish})$
 - Feed coefficient ratio (FCR) = $\text{feed intake (g)}/\text{wet weight gain (g)}$

Results were presented as mean \pm standard error (SE). SPSS 25.0 software (IBM, Chicago, IL, USA) was used for all statistical analyses. All the data were tested for normality, homogeneity and independence of variance prior to ANOVA tests. Student's t-test was used to compare the data between the NLBP and HLBP groups. One-way analysis of variance (ANOVA) followed by Tukey's multiple-range tests were used for analyzing the data among different LBP levels in the 15% α -Starch diet. In all statistical tests used, $p < 0.05$ was considered significantly different.

3 Results

3.1 Growth performance and digestive enzyme activity

The effects of adding LBP to the diet on the growth performance of largemouth bass are shown in Table 3. FBW, WGR, and SGR



were significantly higher in the NLBP group than in the HLBP group ($P < 0.05$). HSI was significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). The FBW, WGR, and SGR of fish in the LBP0.6 group were the highest, and the treatment groups were all significantly higher than in the HLBP group ($P < 0.05$). The quadratic polynomial regression results of *Lycium barbarum* polysaccharide levels with WGR and SGR are shown in Figures 1, 2. HSI was highest in the HLBP group and was significantly higher than in the LBP0.4, LBP0.6, and LBP0.8 groups ($P < 0.05$). FCR was highest in the HLBP group.

Effects of dietary LBP on digestive enzymes activities of the intestinal and liver of fish are shown in Figure 3. The activities of AMS, LPS, and TPS in the intestine were all highest in the LBP0.6 group and significantly higher than in the HLBP group ($P < 0.05$). In the liver, the activities of AMS, LPS, and TPS were all highest in the LBP0.6 group and significantly higher than in the HLBP group ($P < 0.05$).

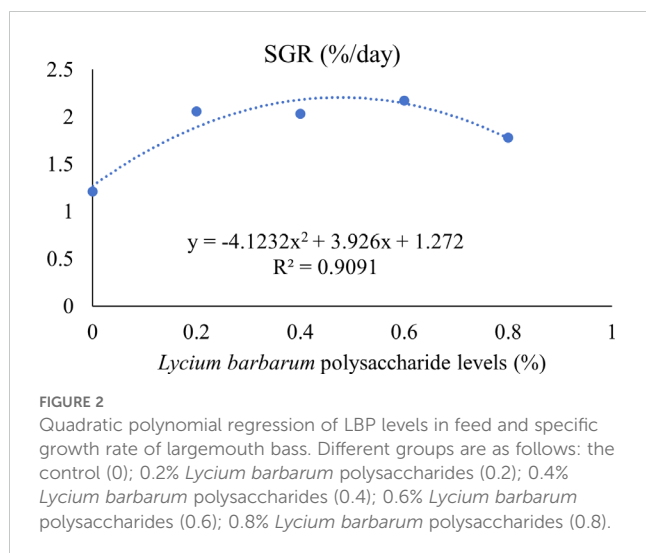
3.2 Serum biochemical parameters and antioxidant enzyme activity

As shown in Table 4, serum levels of TG content and ALT activity were significantly higher in the HLBP group than in the

TABLE 3 Effect of dietary LBP on growth performance and survival of largemouth bass.

Item	NLBP	HLBP	LBP0.2	LBP0.4	LBP0.6	LBP0.8
IBW (g)	41.13 \pm 0.95	42.00 \pm 0.69	41.07 \pm 1.07	43.20 \pm 1.30	41.60 \pm 0.92	41.87 \pm 0.96
FBW (g)	113.69 \pm 0.98	82.86 \pm 0.50 ^{d*}	129.95 \pm 1.25 ^b	134.87 \pm 1.12 ^b	140.55 \pm 0.12 ^a	113.59 \pm 1.98 ^c
WGR (%)	176.43 \pm 1.43	97.40 \pm 3.73 ^{d*}	216.65 \pm 4.55 ^{ab}	212.64 \pm 7.26 ^b	238.21 \pm 7.77 ^a	171.377 \pm 0.79 ^c
SGR (%/d)	1.82 \pm 0.01	1.21 \pm 0.03 ^{c*}	2.06 \pm 0.03 ^a	2.03 \pm 0.04 ^a	2.17 \pm 0.04 ^a	1.78 \pm 0.01 ^b
HSI (%)	3.24 \pm 0.44	4.53 \pm 0.21 ^{a*}	4.14 \pm 0.15 ^{ab}	3.43 \pm 0.29 ^{bc}	3.19 \pm 0.10 ^{bc}	3.14 \pm 0.22 ^c
SR (%)	97.33 \pm 2.30	96.00 \pm 4.00	97.33 \pm 2.30	98.66 \pm 2.30	100.00 \pm 0.00	98.66 \pm 2.30
FCR	0.82 \pm 0.03	0.84 \pm 0.05 ^{a*}	0.81 \pm 0.02 ^b	0.82 \pm 0.03 ^b	0.82 \pm 0.03 ^b	0.83 \pm 0.05 ^{ab}

*" represents statistical difference between the NLBP group and the HLBP group, using Student's t-test ($p < 0.05$). "abcd" represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).



NLBP group ($P < 0.05$). TC and LDL contents were extremely significantly higher in the HLBP group than in the NLBP group ($P < 0.01$). HDL content and AKP activity in the HLBP group were significantly lower than in the NLBP group ($P < 0.05$). In the experimental group, TC and LDL contents were significantly lower than in the HLBP group, and ALT and AST activities were significantly lower than in the HLBP group ($P < 0.05$). The content of HDL and AKP activity were significantly higher in the LBP0.8 group than in the HLBP group ($P < 0.05$).

The antioxidant capacity of the intestine and liver is shown in Figure 4. In the intestine and liver, the activities of T-AOC and GSH-PX were significantly higher in the NLBP group than in the HLBP group ($P < 0.05$); the activity of CAT was extremely significantly higher in the NLBP group than in the HLBP group ($P < 0.01$); the content of MDA was significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). In the intestine and liver, the activities of T-AOC, CAT, GSH-PX, and SOD were significantly higher in the LBP0.6 and LBP0.8 groups than in the HLBP group ($P < 0.05$). In the intestines of the experimental groups, except for the LBP0.2 group, the MDA content was significantly lower than that of the HLBP group ($P < 0.05$). In the liver, MDA content was significantly lower in the experimental groups than in the HLBP group ($P < 0.05$).

3.3 Antioxidant-related and Inflammation-related genes

As shown in Figure 5, the relative expression levels of the *CAT*, *SOD*, and *GPX* genes in the intestines. There was a significant difference in *CAT* gene expression between the NLBP and HLBP groups ($P < 0.05$). The expression of *SOD* gene in the NLBP group was extremely significantly higher than that in the HLBP group ($P < 0.01$). The expression of *CAT*, *SOD*, and *GPX* genes were significantly higher in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$). As shown in Figure 6, the relative expression levels of the *CAT*, *SOD*, and *GPX* genes in the liver. The expression of *CAT* and *SOD* genes were significantly

higher in the NLBP group than in the HLBP group ($P < 0.05$). The expression of *CAT*, *SOD*, and *GPX* genes were highest in the LBP0.8 group and significantly higher than in the HLBP group ($P < 0.05$).

The expression of inflammatory factors in the intestine is shown in Figure 7. *IL-1 β* and *TNF- α* genes expression were significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). *IL-10* and *TGF- β 1* genes expression were significantly higher in the NLBP group than in the HLBP group ($P < 0.05$). The expression of *IL-1 β* , *IL-8*, and *TNF- α* genes were significantly lower in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$). The expression of *IL-10* and *TGF- β 1* genes were significantly higher in the LBP0.6 and LBP0.8 groups than in the HLBP group ($P < 0.05$). The expression of inflammatory factors in the liver is shown in Figure 8. *IL-8* and *TNF- α* genes expression were significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). *TGF- β 1* gene expression was significantly higher in the NLBP group than in the HLBP group ($P < 0.05$). The expression of *IL-1 β* , *IL-8*, and *TNF- α* genes were significantly lower in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$). The expression of *IL-10* and *TGF- β 1* genes were significantly higher in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$).

3.4 Glucolipid metabolism-related genes

The expression of genes related to glucose metabolism in the liver is shown in Figure 9. *GK* gene expression was significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). *PFK* gene expression in the NLBP group was extremely significantly lower than that in the HLBP group ($P < 0.01$). The expression of *GK*, *PFK*, and *G6P* genes were significantly higher in the LBP0.6 and LBP0.8 groups than in the HLBP group ($P < 0.05$). The expression of genes related to lipid metabolism in the liver is shown in Figure 10. *ACC* and *FAS* genes expression were significantly lower in the NLBP group than in the HLBP group ($P < 0.05$). The expression of *ACC*, *CPT-1*, and *FAS* genes were significantly higher in the LBP0.4, LBP0.6, and LBP0.8 groups than in the HLBP group ($P < 0.05$). There was no significant difference in *G6P* and *CPT-1* genes expression between the NLBP and HLBP groups ($P > 0.05$).

4 Discussion

Research has demonstrated that high-carbohydrate diets can have adverse effects on carnivorous fish (Liu Y. et al., 2022; Zheng et al., 2023), and largemouth bass have a low utilization of carbohydrates (Li S. et al., 2020). In this study, a high-carbohydrate diet was found to significantly impair the growth performance of largemouth bass. FBW, WGR, and SGR were significantly lower in the high-carbohydrate diet group than in the low-carbohydrate diet group. This finding suggests that the adaptability of largemouth bass to high-carbohydrate diets may be limited, potentially due to the specificity of its intestinal metabolism and enzymatic activity. Known for their excellent safety and low toxicity, polysaccharides are a type of natural extract from plants

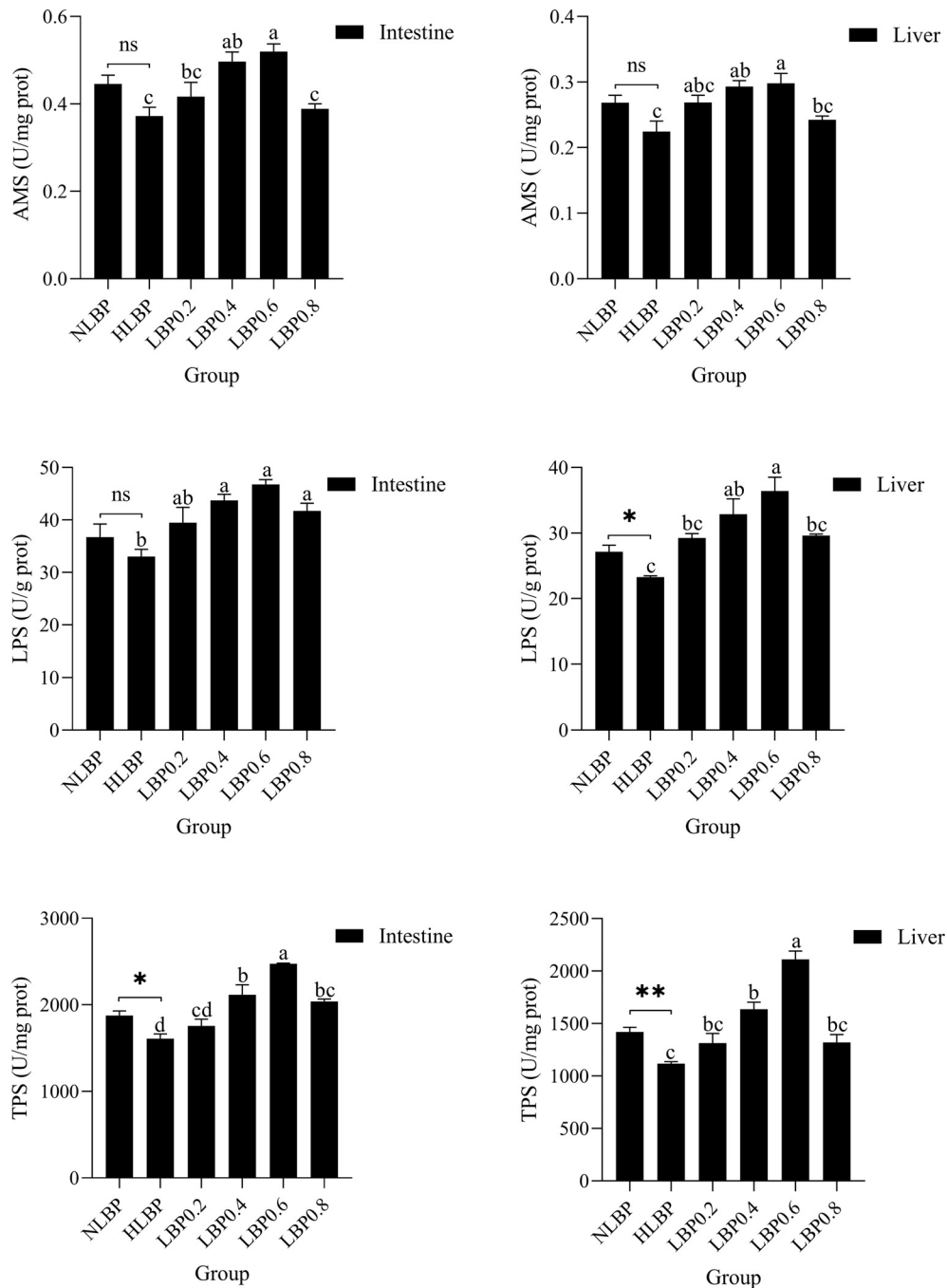


FIGURE 3 Effects of dietary *Lycium barbarum* polysaccharides on AMS, LPS, and TPS activities in the intestinal and liver of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* *p* < 0.05, ** *p* < 0.01 or ns *p* > 0.05). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean ± standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

made up of many monosaccharides with the same or distinct structures joined together by glycosidic linkages (Tian et al., 2019). It is now widely used in the aquaculture industry. Numerous studies have shown that dietary supplementation with 0.5-2.0 g/kg LBP significantly improves the growth performance of aquatic animals such as Turkestan barbel (Sun et al., 2023), spotted sea bass (Huang Z. et al., 2023), Nile tilapia (Zhang X. et al., 2020)

and hybrid grouper (Tan et al., 2019b). In this study, the dietary inclusion of LBP was found to be effective in mitigating the adverse effects of a high-carbohydrate diet on the growth performance of largemouth bass. Dietary addition of 0.6 g/kg LBP showed the best growth performance, even better than the low-carbohydrate dietary group. This is an interesting phenomenon that may be related to the ability of LBP to increase carbohydrate utilization by largemouth

TABLE 4 Effect of dietary LBP on serum biochemical parameters of largemouth bass.

Item	NLBP	HLBP	LBPO.2	LBPO.4	LBPO.6	LBPO.8
TG (mmol/L)	7.73 ± 0.16	10.65 ± 0.75 ^{a*}	8.28 ± 0.45 ^{ab}	5.77 ± 0.67 ^{bc}	5.41 ± 0.47 ^c	5.09 ± 0.49 ^c
TC (mmol/L)	8.54 ± 0.08	13.15 ± 0.57 ^{a**}	10.78 ± 0.27 ^b	8.24 ± 0.24 ^c	8.65 ± 0.63 ^c	8.28 ± 0.28 ^c
HDL (mmol/L)	2.58 ± 0.17	2.07 ± 0.03 ^{b*}	2.38 ± 0.13 ^{ab}	2.77 ± 0.01 ^{ab}	2.65 ± 0.05 ^{ab}	2.99 ± 0.34 ^a
LDL (mmol/L)	2.64 ± 0.09	4.35 ± 0.25 ^{a**}	2.31 ± 0.27 ^b	2.23 ± 0.38 ^b	2.42 ± 0.07 ^b	2.26 ± 0.35 ^b
ALT (U/L)	10.82 ± 0.52	17.09 ± 1.98 ^{a*}	9.68 ± 1.29 ^b	5.92 ± 0.89 ^{bc}	3.26 ± 0.38 ^c	3.43 ± 0.75 ^c
AST (U/L)	96.99 ± 2.61	135.49 ± 14.41 ^a	87.38 ± 12.69 ^b	71.33 ± 4.54 ^{bc}	47.91 ± 8.76 ^{bc}	35.93 ± 7.67 ^c
AKP (U/L)	28.94 ± 1.71	16.12 ± 3.49 ^{c*}	24.24 ± 1.41 ^{bc}	27.05 ± 0.44 ^{abc}	41.15 ± 5.06 ^{ab}	49.33 ± 9.64 ^a

“*” represents statistical difference between the NLBP group and the HLBP group, using Student’s t-test (* $p < 0.05$ or ** $p < 0.01$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean ± standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBPO.2); 0.4% *Lycium barbarum* polysaccharides (LBPO.4); 0.6% *Lycium barbarum* polysaccharides (LBPO.6); 0.8% *Lycium barbarum* polysaccharides (LBPO.8).

bass (Ooi et al., 2004). LBP may have the potential to enhance carbohydrate metabolism and improve energy utilization, a function which could be achieved by modulating the intestinal microenvironment and directly influencing metabolic pathways. Furthermore, it has been demonstrated that plant extracts can enhance lipid metabolism in fish (Xiao et al., 2017). Another significant role of LBP may be related to their impact on lipid metabolism. In this study, LBP addition above 0.4 g/kg was effective in reducing the hepatosomatic index of largemouth bass. This suggests that LBP may reduce hepatic fat accumulation by regulating lipid metabolism. These data suggest that LBP positively regulates the growth performance of largemouth bass. Most studies show that improvements in growth performance and feed consumption efficiency are correlated with increased digestive enzyme activity (Najdegerami et al., 2017; Zheng et al., 2018; Huang et al., 2020). In this experiment, the addition of LBP significantly increased feed utilization by largemouth bass, and the addition of 0.4–0.6 g/kg of LBP significantly increased the digestive enzyme activity of largemouth bass. Polysaccharides can enhance the digestive enzyme activity of aquatic animals (Wu et al., 2020; Yu et al., 2022); this may be due to their ability to influence the structure of the intestinal flora of aquatic organisms (Liu et al., 2020). Firstly, several species in the gut have the ability to produce exogenous digestive enzymes directly, which aids in the host’s improvement of digestion (Latorre et al., 2016). Furthermore, polysaccharides may be broken down by intestinal bacteria and transformed into healthy compounds like short-chain fatty acids. In addition to enhancing the action of digestive enzymes and controlling the pH of the animal intestines, these chemicals also benefit intestinal epithelial cells, which in turn promotes intestinal function (Huang Z. et al., 2023). In this study, the addition of 0.6 g/kg LBP significantly ameliorated the negative effects of a high-carbohydrate diet on largemouth bass and significantly improved growth performance and digestibility.

The blood absorbs and digests the nutrients in the diet. As a result, serum biochemical parameters can reveal an aquatic animal’s health in addition to its clinical and physiological conditions (Mu et al., 2018; Abdel-Latif et al., 2021). Variations in those factors have shown how aquatic animals may adapt to different food formulations

and surroundings (Li M. et al., 2020), as well as how such changes might influence their immune systems (Chekani et al., 2021; Zhong et al., 2024). In the present study, a high-carbohydrate diet significantly increased serum TG, TC, and LDL levels in largemouth bass. This is consistent with metabolic disorders observed in other aquatic animals under similar dietary conditions (Jia et al., 2024). Such alterations in metabolism may lead to decreased energy utilization efficiency and fat accumulation, thereby impacting the health and growth of fish. This suggests that a high carbohydrate diet appears to negatively affect glycolipid metabolism in largemouth bass. In general, HDL facilitates the transport of cholesterol from peripheral tissues to hepatic cells for further metabolism, whereas LDL mediates the transfer of cholesterol from the liver to various tissues. But elevated LDL levels are not a good sign (Jafari et al., 2018). Addition of LBP to a high-carbohydrate diet effectively reduced serum TG, TC, and LDL levels, suggesting that LBP can help largemouth bass utilize carbohydrates efficiently and regulate glycolipid metabolism. Serum ALT and AST activities are widely recognized as important indicators of liver damage, reflecting the extent of hepatocellular injury (Liu et al., 2012). In addition, serum AKP activity also reflects the health status of the liver in largemouth bass (Huang H. et al., 2023). In this study, the activities of serum ALT, AST, and AKP demonstrate that a high-carbohydrate diet can adversely impact the liver health of largemouth bass. However, the supplementation with LBP effectively mitigates these negative effects. This may be associated with the hepatoprotective and anti-inflammatory effects of LBP, suggesting their potential application in the prevention of liver diseases. High-carbohydrate diets have the potential to negatively impact the antioxidant capacity of largemouth bass, potentially leading to increased oxidative stress and associated health issues (Lin et al., 2018; Guo et al., 2020). SOD, CAT, T-AOC, GSH-PX, and MDA were often used to assess antioxidant capacity in fish (Tan et al., 2019a). SOD, CAT, and GSH-PX were important antioxidant enzymes and T-AOC directly reflected the ability of fish to scavenge oxygen free radicals, while MDA content showed the severity of oxidative stress (Tan et al., 2016). In the present study, a high-carbohydrate diet significantly decreased the activity of antioxidant enzymes and the expression levels of antioxidant-related genes in both the intestine and liver. This

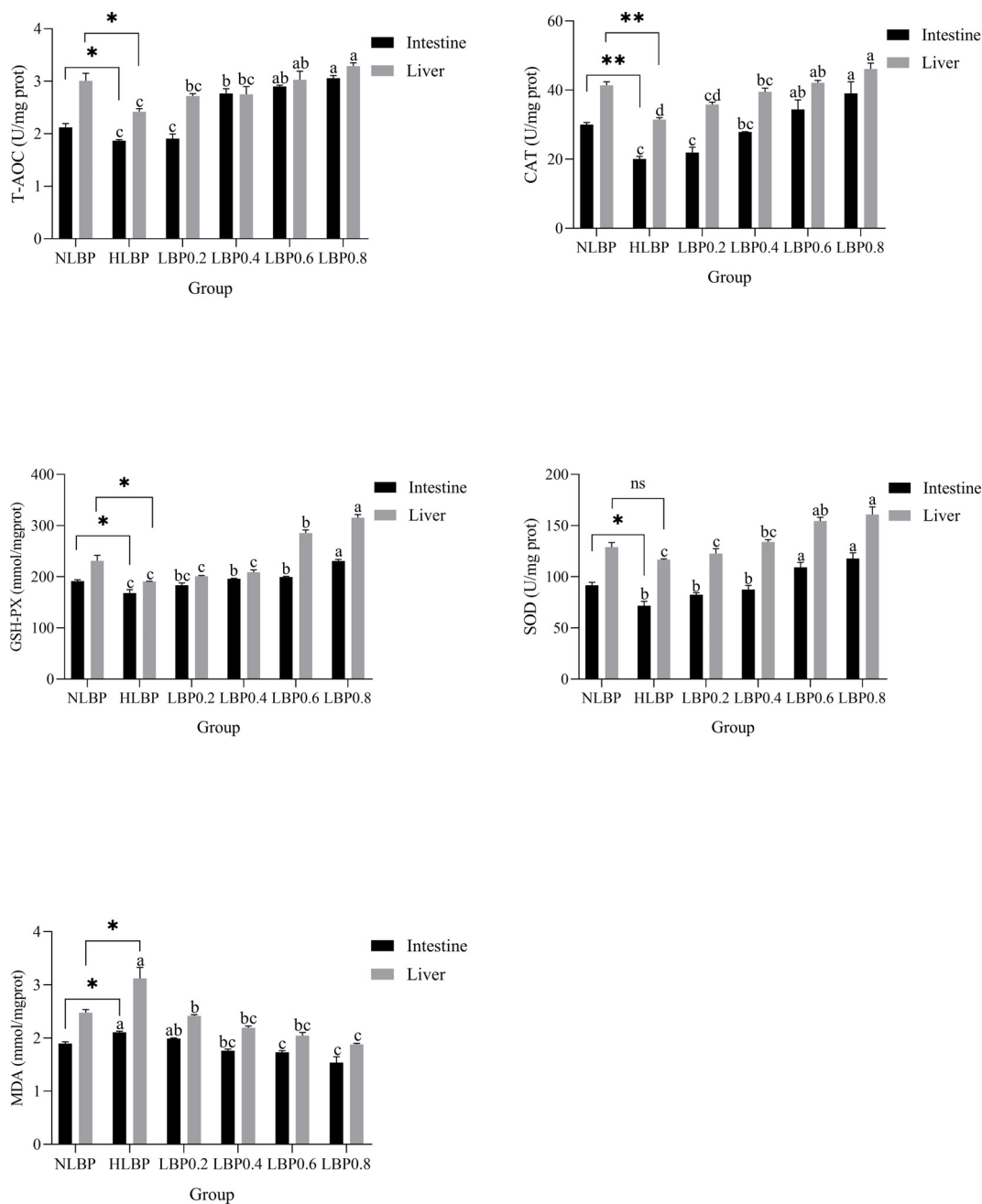


FIGURE 4
 Effects of dietary *Lycium barbarum* polysaccharides on T-AOC, CAT, GSH-PX, SOD activities and MDA content in the intestinal and liver of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* $p < 0.05$, ** $p < 0.01$ or ns $p > 0.05$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

indicates that the high carbohydrate diet significantly impacted the antioxidant capacity of largemouth bass. However, the addition of LBP significantly improved the situation. According to some research, the *LBP* exhibited hepatoprotective and antioxidant abilities, improving the liver damage caused by carbon tetrachloride by raising the activity of antioxidant enzymes in common carp (Liu et al., 2015). This has similar conclusions to the present study. In the present study, the supplementation of LBP was found to significantly

enhance the activities of antioxidant enzymes and upregulate the expression of antioxidant genes in both the intestinal and hepatic tissues of largemouth bass. These findings suggest that LBP has the potential to markedly improve the antioxidant capacity of largemouth bass when they are fed a high-carbohydrate diet.

In aquaculture species, eels, Nile tilapia, and largemouth bass experienced intestinal and hepatic inflammation when fed a diet high in carbohydrates (Lin et al., 2018; Shi et al., 2022; Wang et al.,

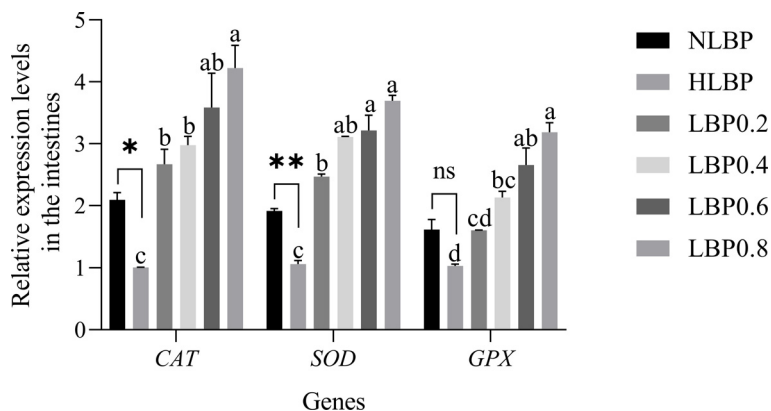


FIGURE 5
The relative expression levels of *CAT*, *SOD*, and *GPX* genes in the intestines of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* $p < 0.05$, ** $p < 0.01$ or ns $p > 0.05$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

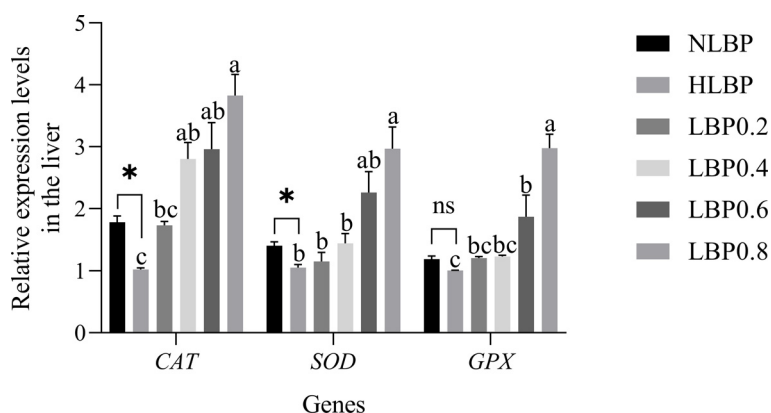


FIGURE 6
The relative expression levels of *CAT*, *SOD*, and *GPX* genes in the liver of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* $p < 0.05$, ** $p < 0.01$ or ns $p > 0.05$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

2022b). In summary, inflammation is a healthy physiological process that restores tissue vitality and removes foreign particles interfering with tissue homeostasis (Kiecolt-Glaser et al., 2010). However, when proinflammatory chemicals have the upper hand, persistent inflammation can lead to tissue damage (Shimoda et al., 2016). Pro-inflammatory cytokines, including, *IL-1 β* , *IL-8*, and *TNF- α* are useful indicators for assessing inflammation and have significant functions in fish immunological response (Zhang et al., 2018). Anti-inflammatory factors such as *IL-10* and *TGF- β 1* can likewise be used as indicators of the inflammatory response in fish (Tan et al., 2019a). In the present study, chronic high-carbohydrate diets significantly increased the expression of pro-inflammatory factors in the intestine and liver, in contrast to significantly decreasing the expression of anti-inflammatory factors. This suggests that a high-carbohydrate diet may exacerbate tissue

inflammation by promoting the expression of inflammatory factors, thereby posing a threat to the intestinal and hepatic health of fish. Likewise, some studies show that a diet containing 15% starch induced intestinal inflammation in largemouth bass (Zhou et al., 2021). A high-carbohydrate diet may trigger inflammatory responses by affecting the balance of gut microbiota, increasing intestinal permeability, or directly stimulating immune cells. In addition, it has been shown that oxidative stress leads to an inflammatory response in the body (Zhang et al., 2022), which is similar to the conclusions obtained in this study. The antioxidant properties of LBP may contribute to their anti-inflammatory effects. Oxidative stress has been widely recognized as associated with inflammatory states, and antioxidants can alleviate inflammation induced by oxidative stress. Therefore, LBP may indirectly suppress inflammatory responses by enhancing

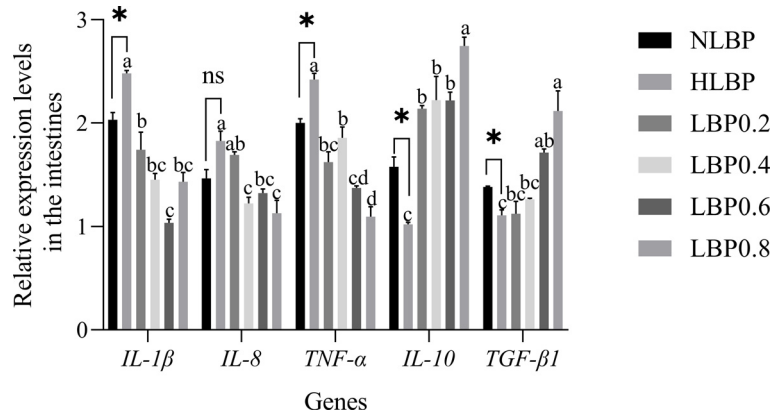


FIGURE 7
The relative expression levels of *IL-1β*, *IL-8*, *TNF-α*, *IL-10*, and *TGF-β1* genes in the intestines of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* *p* < 0.05, ** *p* < 0.01 or ns *p* > 0.05). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean ± standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

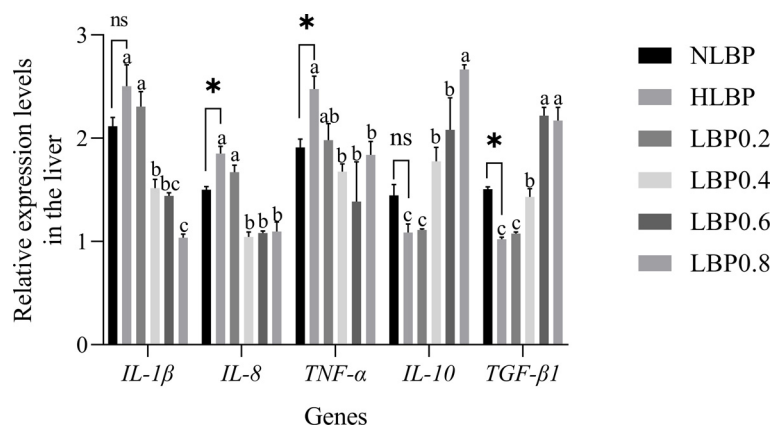


FIGURE 8
The relative expression levels of *IL-1β*, *IL-8*, *TNF-α*, *IL-10*, and *TGF-β1* genes in the liver of largemouth bass. “*” represents statistical difference between the NLBP group and the HLBP group, using Student’s *t*-test (* *p* < 0.05, ** *p* < 0.01 or ns *p* > 0.05). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean ± standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

the activity of antioxidant enzymes and reducing oxidative stress. Interestingly, in this experiment, the expression of pro-inflammatory factors in the intestine and liver of largemouth bass decreased significantly and the expression of anti-inflammatory factors increased significantly with increasing LBP addition. This shows the same trend as antioxidant-related genes and there seems to be a dose effect. This also seems to validate oxidative stress as one of the factors contributing to the body’s inflammatory response. In conclusion, LBP was effective in ameliorating the largemouth bass intestinal and liver inflammatory responses induced by a high-carbohydrate diet.

Fish that consume excessive starch may develop hyperglycemia and glycogen accumulation (Zhang et al., 2019). In this study, a high-carbohydrate diet significantly increased the expression of *GK* and *PFK* genes, which are key regulators of glucose metabolism. The

upregulation of these genes suggests that consumption of a high-carbohydrate diet enhances glucose metabolic activity. But in comparison to growth performance, largemouth bass did not effectively utilize carbohydrates. This may indicate issues with metabolic efficiency or potential inhibition of related glucose metabolic pathways. Dietary addition of LBP can effectively regulate the abundance of intestinal flora, thereby affecting the ability of organisms to metabolize glycolipids (Cui et al., 2020; Zhu et al., 2020). In this study, the addition of LBP to a high-carbohydrate diet significantly increased the expression of glucose metabolism genes and was highest in the LBP0.6 group. This suggests that the addition of appropriate dose of LBP can help largemouth bass improve the utilization of carbohydrates. ACC and FAS are the key enzymes involved in fatty acid synthesis. Acetyl-CoA is carbonylated to malonyl-CoA by ACC, and malonyl-CoA is

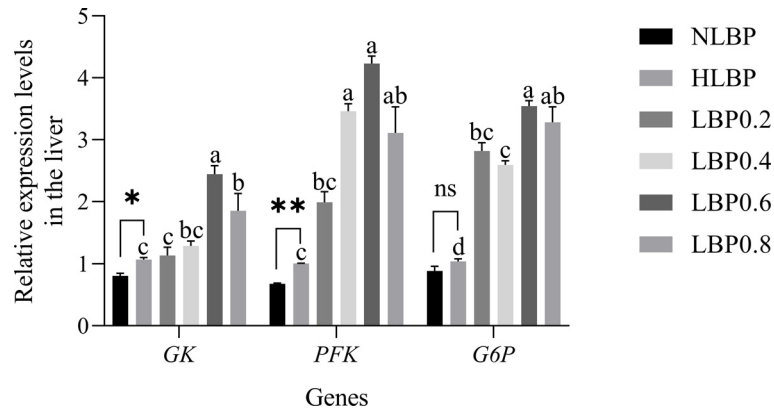


FIGURE 9

The relative expression levels of *GK*, *PFK*, and *G6P* genes in the liver of largemouth bass. “**” represents statistical difference between the NLBP group and the HLBP group, using Student’s t-test (* $p < 0.05$, ** $p < 0.01$ or ns $p > 0.05$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

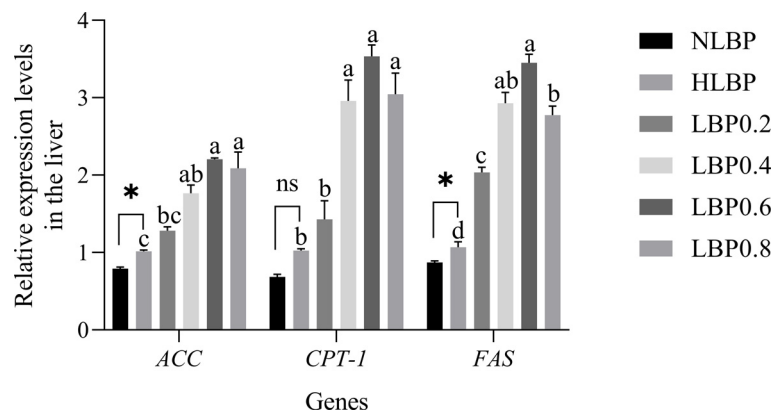


FIGURE 10

The relative expression levels of *ACC*, *CPT-1*, and *FAS* genes in the liver of largemouth bass. “**” represents statistical difference between the NLBP group and the HLBP group, using Student’s t-test (* $p < 0.05$, ** $p < 0.01$ or ns $p > 0.05$). “abcd” represents statistical difference among different LBP levels in the high glucose feed diet. Data expressed as a mean \pm standard error. Different groups are as follows: 10% glucose feed without LBP (NLBP); 15% glucose feed without LBP (HLBP); 0.2% *Lycium barbarum* polysaccharides (LBP0.2); 0.4% *Lycium barbarum* polysaccharides (LBP0.4); 0.6% *Lycium barbarum* polysaccharides (LBP0.6); 0.8% *Lycium barbarum* polysaccharides (LBP0.8).

converted to palmitic acid by FAS, which is then esterified to triglycerides (Wu and Huang, 2020). One of the important enzymes in lipolytic metabolism is CPT-1. PPAR- α mediates CPT1’s catalytic conversion of lipoyl CoA to lipoyl carnitine, which starts the mitochondrial β -oxidation of long-chain fatty acids (Song et al., 2015). In the present study, the high-carbohydrate diet significantly increased the expression of *ACC* and *FAS* genes, but there was no significant difference in the expression of *CPT-1* gene. This suggests that a high-carbohydrate diet increased the risk of lipid deposition in the liver of largemouth bass. This is not good information for the state of health of largemouth bass. However, the addition of LBP to a high-

carbohydrate diet can effectively alleviate this condition. In this study, the addition of LBP significantly increased the expression of lipid synthesis genes and lipolysis genes, which appeared to reach a state of equilibrium, which appeared to be more favorable to largemouth bass when comparing growth performance. This suggests that LBP may reduce adverse lipid accumulation by modulating the balance between lipid synthesis and breakdown, thereby maintaining liver health. This balance may be due to the role of *Lycium barbarum* polysaccharides in regulating lipid metabolism, particularly through their potential involvement in PPAR- α mediated metabolic pathways. In summary, LBP can help largemouth bass utilize high carbohydrates efficiently.

Conclusions

In summary, high-carbohydrate diets can negatively affect the growth performance, digestibility, immune status, and metabolism of largemouth bass. However, the addition of LBP to the high-carbohydrate diet can effectively improve this situation, and LBP can effectively improve the growth performance, digestive ability, immune status, and glycolipid metabolism of largemouth bass. Under the conditions of this experiment, the most suitable additive amount of LBP was 0.6 g/kg.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Shanghai Ocean University's ethical guidelines. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

LQ: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. YH: Data curation, Formal analysis, Investigation, Software, Writing – review & editing. GZ: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

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