frontiers | Frontiers in Marine Science

TYPE Original Research
PUBLISHED 13 March 2023
DOI 10.3389/fmars.2023.1149887

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Aquatic Physiology, a section of the journal Frontiers in Marine Science

RECEIVED 23 January 2023
ACCEPTED 27 February 2023
PUBLISHED 13 March 2023

CITATION
Li J, Wang Z, Cao X, Wang J, Gong Y, Wang X, Lai W, Bu X, Zheng J, Mai K and Ai Q (2023) Effects of supplemental mixed bile acids on growth performance, body composition, digestive enzyme activities, skin color, and flesh quality of juvenile large yellow croaker (*Larimichthys crocea*) in soybean oil based diet. *Front. Mar. Sci.* 10:1149887. doi: 10.3389/fmars.2023.1149887

Effects of supplemental mixed bile acids on growth performance, body composition, digestive enzyme activities, skin color, and flesh quality of juvenile large yellow croaker (*Larimichthys crocea*) in soybean oil based diet

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Now the replacement of fish oil (FO) with vegetable oils (VOs) has been broadly applied in aquatic feed, but studies reported that there were negative effects on growth, skin color, flavor and muscle texture. A 10-week feeding trial was conducted to investigate the effects of dietary mixed bile acids (BA) on growth performance, body composition, digestive enzyme activities, skin color and flesh quality of juvenile large yellow croaker (initial weight, 13.10 ± 0.18 g). Four iso-nitrogenous and iso-lipidic experimental diets were formulated and designated as soybean oil (SO), SO supplemented with 300 (BA300), 600 (BA600), and 1200 (BA1200) mg/kg bile acids. Two hundred and forty fish were randomly allocated into 12 floating net cages (1 m × 1 m × 1.5 m) that were located at marine fishing rafts. Each diet was randomly distributed in triplicate (three replicates per treatment, 20 fish per replicate). Fish were hand-fed to apparent satiation twice daily (05:30 and 17:30) for 10 weeks. Results showed that specific growth rate presented quadratic pattern with supplemental bile acids level, peaking at BA600 group. Meanwhile, feed conversion rate of cultured fish was significantly improved in BA600 group ($P < 0.05$). The redness (a*) of dorsal and lateral line skin and the yellowness (b*) of abdominal skin showed significantly quadratic pattern with the increase of supplemental BA level ($P < 0.05$), peaking at BA600 group. In terms of dorsal muscle texture, springiness showed a decreasing trend in significantly linear pattern with the increase of supplemental BA level, bottoming at BA600 group. However, cohesiveness and gumminess were significantly linear increased with the increase of supplemental BA level ($P < 0.05$). No significant differences were observed in

lipase, amylase, and trypsin activities ($P > 0.05$). Total proportion of muscle n-3LCPUFA showed a linearly increasing trend with the increase of supplemental BA level. Muscle TG content was linearly increased with the increase of supplemental BA level ($P < 0.05$), and significant differences occurred as compared to fish fed diets with SO when supplemental BA level were reached 600 mg/kg and 1200 mg/kg ($P < 0.05$). The gene expression of acyl-CoA oxidase (*aco*) was significantly decreased in fish fed diets supplemented with 600 mg/kg bile acids compared with 300 mg/kg other than those fed diets with SO. In conclusion, these results suggested that mixed bile acids supplemented to SO-based diets could improve feed conversion ratio, skin color and flesh quality to some extent.

KEYWORDS

mixed bile acids, growth performance, body composition, digestive enzyme activities, flesh quality, gene expression, *Larimichthys crocea*

1 Introduction

In recent years, capture fisheries are gradually declining, which induces a steady increase in aquaculture production for meeting global demands for seafood (Watanabe, 2002; Turchini et al., 2010; Fawole et al., 2021). Thus, the demand for commercial aquatic feeds continue to increase. As an important lipid source in aquatic feeds, fish oil (FO) is abundant in n-3 polyunsaturated fatty acids, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Yu et al., 2017), which are indispensable for growth and development of farmed marine animals. However, with the rapid expansion of aquaculture and the sharp increase of aquatic feed, the contradiction of FO between supply and demand becomes more and more prominent (Nasopoulou and Zabetakis, 2012). Compared with FO, vegetable oils (VOs) have many advantages including easy availability, relatively stable output and acceptable price (Bell et al., 2005; Tan et al., 2016), therefore they are considered as the best alternative lipid sources in aquafeed (Montero et al., 2015). Some studies reported that partial replacement of FO with VOs had no effects on growth and feed utilization in large yellow croaker (Duan et al., 2014), yellowtail (Aoki et al., 2000), Atlantic salmon (Bell et al., 2003), gilthead seabream (Menoyo et al., 2004; Fountoulaki et al., 2009), turbot (Regost et al., 2003b), cobia (Trushenski et al., 2011). However, high level VOs replacing FO had significantly negative effects on growth performance, body composition, fatty acid profiles, skin color, flavor and muscle texture in turbot (Regost et al., 2003a), gilthead seabream (Fountoulaki et al., 2009), red spotted grouper (Wang et al., 2016), large yellow croaker (Mu et al., 2018). Therefore, it is necessary to alleviate or eliminate the negative effects of FO substituted with VOs by nutrition regulation.

Bile acids are the main component of bile and synthesized in liver from cholesterol (Houten et al., 2006; Hofmann and Hagey, 2008). They have been well recognized to be able to emulsify lipids (Wang and Hartsuck, 1993; Alrefai and Gill, 2007; Romano et al., 2020), activate intestinal lipase (Adhami et al., 2017; Romano et al., 2020; Li et al., 2021b) and combine to long chain fatty acids to form a water-soluble complex (Einarsson et al., 1991) so as to improve lipids efficiency. Moreover, bile acids play vital role in emulsification, digestion and absorption of lipids. Meanwhile, they are considered as signaling molecules to regulate metabolism of triglyceride, cholesterol and maintain energy and glucose homeostasis (Insull, 2006; Nguyen and Bouscarel, 2008; Pols et al., 2011; Swann et al., 2011; Burrin et al., 2013; Di Ciaula et al., 2017; Molinaro et al., 2018). Previous studies in mammals and aquatic animals have shown that bile acids could effectively promote growth, improve lipids metabolism and reduce fat accumulation such as broiler (Lai et al., 2018; Ge et al., 2019), grass carp (Zhou et al., 2018), tilapia (Jiang et al., 2018), large yellow croaker (Du et al., 2017; Ding et al., 2020), largemouth bass (Yu et al., 2019; Yin et al., 2021) and improve body quality such as broiler (Lai et al., 2018), Wagyu heifer (Irie et al., 2011), grass carp (Zeng et al., 2017) and large yellow croaker (Yi et al., 2013). Given the functional properties of bile acids, dietary supplementary bile acids are gaining increasing concern in fish and providing the feasibility for improving the negative effects described above of FO replaced by VOs.

Large yellow croaker (*Larimichthys crocea*)is an important marine fish species with high economic value which has been widely farmed in China (Duan et al., 2014; Du et al., 2017; Ding et al., 2020; He et al., 2022). Previous studies indicated that VOs replacing FO had negative effects on growth, skin color and flesh quality etc. (Yi et al., 2013; Mu et al., 2018), which hindered the development of aquaculture industry and consumer market of large yellow croaker to some extent. In the previous study of our laboratory, supplemental chenodeoxycholic acid (CDCA) in diet replacing fish oil with soybean oil could significantly improve growth performance (Du et al., 2017). However, on the one hand, the price of CDCA is higher than mixed bile acids and it hasn't been extensively applied in aquaculture. On the other hand, no study was conducted on flesh quality of large yellow croaker in above-mentioned study. Considering this, the purpose of the study was to comprehensively investigate the effects of the exogenous supplementation of mixed bile acids on growth performance, skin color and flesh quality of large yellow croaker.

2 Materials and methods

2.1 Ethics statement

The present study was conducted in strict accordance with the Management Rule of Laboratory Animals (Chinese Order No.676 of the State Council, revised 1 March 2017) and approved by the Committee on the Ethics of Animal Experiments of Ocean University of China.

2.2 Feed ingredients and diets formulation

Four iso-nitrogenous (42% crude protein) and iso-lipidic (12% crude lipid) experimental diets were formulated, including SO (formulation diet with soybean oil as the lipid source), BA300 (formulation diet with SO supplemented with 300 mg/kg mixed bile acids), BA600 (formulation diet with SO supplemented with 600 mg/kg mixed bile acids), and BA1200 (formulation diet with SO supplemented with 1200 mg/kg mixed bile acids). White fish meal, krill meal, and soybean meal were used as the main protein sources. Soybean oil was used as the main oil source. Ingredients were grinded to fine powder and mixed thoroughly to make pellets using pellet mill (EL-220, Haiyang City Huatong Machinery Co., Ltd., Shandong, China). After drying, diets were sieved into a proper size (diameter: 2 mm, length: 8 mm). Analysis of dry matter (105 C, 24 h), crude protein (Kjeldahl nitrogen × 6.25) and crude lipid (ether extraction by Soxhlet method) in experimental diets were performed according to the standard methods of Association of Official Analytical Chemists (AOAC, 2005). Feed formulation and proximate composition are presented in Table 1. All formulated diets were packed in separate bags and stored at -20° until further use.

2.3 Fish and experimental procedures

Hatchery produced juvenile large yellow croaker were purchased from Xiangshan Harbor Aquatic Seeds Company (Ningbo, China). Before the feeding trail, fish were reared for 2 weeks to acclimate the experimental diet and rearing condition. After acclimation, two hundred and forty fish (initial weight, 13.10 ± 0.18 g) were randomly allocated into 12 floating net cages (1 m × 1 m × 1.5 m) that were located at marine fishing rafts of Ningbo Marine Fishery Science and Technology Innovation Base. Each diet was randomly distributed in triplicate (three replicates per treatment, 20 fish per replicate). Fish were hand-fed to apparent satiation twice daily (05:30 and 17:30) for 10 weeks. During the feeding period, the water salinity, temperature, and dissolved oxygen were maintained at 25-28‰, 22-29°, 6.2-7.5 mg/L, respectively.

2.4 Sample collection

At the end of the experiment, all fish were fasted for 24 h and anesthetized with diluted MS-222 (Sigma-Aldrich, USA) before sampling. All fish were counted and weighed for measuring the survival rate、specific growth rate, respectively. Three fish from each cage were randomly sampled for the analysis of the body composition. The liver and viscera of six fish from each cage were weighed for measuring the hepatosomatic index and viscerosomatic index. Blood samples of three fish from each cage were obtained from the caudal vein using heparinized syringes and centrifuged at 3,000×*g* at 4°C for 10 min. The plasma was collected and stored at -80°C for subsequent analysis. Dorsal muscle and mid-intestine samples were flash-frozen in liquid nitrogen for determination of muscle quality and enzyme activities, respectively.

2.5 Body composition analysis

Proximate compositions of diets and whole fish were both analyzed by the standard methods of Association of Official Analytical Chemists (AOAC, 2005). Moisture was measured by drying at 105°C until constant weight in the oven. Crude protein (nitrogen × 6.25) was determined by the micro-Kjeldahl method using an Auto Kjeldahl System (FOSS KT260, Switzerland). Crude lipid was measured by solvent extraction using a Soxtec System (Soxtec System HT6; Tecator, Höganäs, Sweden). Ash was analyzed by combustion at 550°C for 4 h.

2.6 Skin color measurement

Skin color measurements were performed with a portable Minolta Chroma Meter CR-400 (Minolta, Osaka, Japan). According to CIE (CIE, 1976), the color parameters were L* for lightness, a* for redness or greenness, and b* for yellowness or blueness, respectively.

2.7 Dorsal muscle texture analysis

Texture analysis (hardness, adhesiveness, springiness, cohesiveness, gumminess, chewiness, resilience) was performed by a texture analyzer (TMS-PRO, FTC, USA). A texture profile analysis (TPA) was conducted using an 8-mm cylinder probe. The test parameters were set as follows: 0.1 N with the initial force, 30 mm/min of compression speed, and 60% of deformation of the original length (Gines et al., 2004).

2.8 Biochemical analysis of plasma and muscle

Plasma total bile acid (TBA), total cholesterol (TC), glucose (GLU), total protein (TP) content and muscle triglyceride (TG) level were measured by colorimetric enzymatic methods using commercial kits (Nanjing Jiancheng Bioengineering Institute, China).

TABLE 1 Formulation and proximate composition of the experimental diets.

Ingredients (%)	SO	BA300	BA600	BA1200
White fish meal[1]	37.00	37.00	37.00	37.00
Krill meal[1]	5.00	5.00	5.00	5.00
Soybean meal[1]	23.20	23.20	23.20	23.20
Wheat flour[1]	18.00	18.00	18.00	18.00
Soybean oil	7.50	7.50	7.50	7.50
Choline chloride	0.20	0.20	0.20	0.20
Soybean lecithin	2.00	2.00	2.00	2.00
Vc polyphosphate	0.05	0.05	0.05	0.05
$Ca(H_2PO4)_2$	2.00	2.00	2.00	2.00
Vitamin premix[2]	2.00	2.00	2.00	2.00
Mineral premix[3]	1.00	1.00	1.00	1.00
Microcrystalline cellulose	0.90	0.87	0.84	0.78
Mould inhibitor	0.10	0.10	0.10	0.10
Attractant[4]	1.00	1.00	1.00	1.00
Ethoxyquin	0.05	0.05	0.05	0.05
Mixed bile acids[5]	0.00	0.03	0.06	0.12
Proximate analysis (% dry matter)				
Dry matter (%)	86.27	87.15	87.34	87.04
Crude protein (%)	42.52	42.13	42.53	42.45
Crude lipid (%)	12.65	12.44	12.18	12.15

[1]White fish meal (74.00% crude protein, 7.84% crude lipid); krill meal (64.86% crude protein, 8.0% crude lipid); soybean meal (54.08% crude protein, 0.35% crude lipid); bread flour (21.2% crude protein, 0.34% crude lipid). These ingredients were provided by Great-Seven Biotechnology Co., Ltd., Shandong, China.
[2]Vitamin premix (mg/kg diet), retinal acetate, 32; cholecalciferol, 5; alpha-tocopherol, 240; menadione, 10; thiamin, 25; riboflavin, 45; pyridoxine HCl, 20; vitamin B12, 10; pantothenic acid, 60; folic acid, 20; niacin 200; biotin, 60; inositol, 800; microcrystalline cellulose, 13473. Vitamin C was supplied in the form of vitamin C polyphosphate.
[3]Mineral premix (mg/kg diet), $MgSO_4{\cdot}7H_2O$, 1200; $CuSO_4{\cdot}5H_2O$, 10; $FeSO_4{\cdot}H_2O$, 80; $ZnSO_4{\cdot}H_2O$, 50; $MnSO_4{\cdot}H_2O$, 45; $CoCl_2{\cdot}6H_2O$(1%), 50; Na_2SeO_3(1%), 20; $Ca(IO_3)_2{\cdot}6H_2O$(1%), 60; Zeolite powder, 13485.
[4]Attractant: glycine and betaine.
[5]Mixed bile acids(≥ 95%, Hyodeoxycholic acid+Hyocholic acid ≥ 77%;chenodeoxycholic acid ≥ 17%)were provided by Shandong Longchang Animal Health Product Co., Ltd, Shandong, China.

2.9 Digestive enzyme activities assay

The intestine of fish was weighed (0.2 g) and then homogenized in 2 mL ice-cold PBS followed by centrifugation at 3,000×*g* for 10 min. The supernatant was subject to digestive enzyme activities assay. Lipase, amylase, and trypsin activities were measured by colorimetric enzymatic methods using commercial kits (Nanjing Jiancheng Bioengineering Institute, China). The total protein was measured by using commercial kits (Nanjing Jiancheng Bioengineering Institute, China).

2.10 Real-time quantitative polymerase chain reaction

In the present study, the sequences of primers were designed based on nucleotide sequences from GeneBank using software Primer Premier 5, and the method of total RNA extraction and complementary DNA (cDNA) synthesis were as described in the previous publication (Li et al., 2021a). qPCR measurements were performed in a total volume of 20 μL, containing 1 μL of each primer, 2 μL of cDNA product, 10 μL of SYBR-Premix ExTaqII (Takara, Japan) and 6 μL of RNA-free water and was carried out in a CFX Connect Real-Time System (Bio-Rad). The amplification procedure was employed as follows: 95°C for 2 min, followed by 39 cycles of 95°C for 10 s, 58°C for 10 s, and 72°C for 20 s. Primer of each gene for RT-qPCR was designed according to mRNA sequences of large yellow croaker, amplification efficiencies of all genes ranged from 0.95 to 1.05, and β-actin was chosen as the internal control. The expression level of genes was calculated and normalized using the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen, 2001). The primers were referred in previous study and listed in Table 2.

TABLE 2 Gene primers sequence used for real-time PCR.

Gene	Forward (5′-3′)	Reverse (5′-3′)	References (Genebank No.)
cd36	GAGCATGATGGAAAATGGTTCAAAG	CTCCAGAAACTCCCTTTCACCTTAG	Yan et al., 2015
fas	CAGCCACAGTGAGGTCATCC	TGAGGACATTGAGCCAGACAC	JX456351
scd	AAAGGACGCAAGCTGGAACT	CTGGGACGAAGTACGACACC	Cai et al., 2016
cpt1	GCTGAGCCTGGTGAAGATGTTC	TCCATTTGGTTGAATTGTTTACTGTCC	JX434612
aco	AGTGCCCAGATGATCTTGAAGC	CTGCCAGAGGTAACCATTTCCT	JX456348

cd36, cluster of differentiation 36; fas, fatty acid synthase; scd, stearoyl-coenzyme A desaturase; cpt1, carnitine palmitoyl transferase 1; aco, acyl-CoA oxidase.

2.11 Calculations and statistical analysis

$$Survival\ rate(SR) = N_t/N_0$$

$$Specific\ growth\ rate\left(SGR\text{‹}\%\ day^1\right) = (Ln\ W_t - Ln\ W_0) \times 100/d$$

$$Feed\ intake\ rate(FI\text{‹}\%) = feed\ intake \times 100/((W_0 + W_t)/2)$$

$$Feed\ conversion\ ratio(FCR) = feed\ intake/total\ wet\ weight\ gain$$

$$Hepatosomatic\ index(HSI\text{‹}\%) = liver\ weight \times 100/body\ weight$$

$$Visceral\ somatic\ index(VSI\text{‹}\%) = viscera\ weight \times 100/body\ weight$$

$$Condition\ factor(K\text{‹}\%) = (body\ weight\text{‹}\ g) \times 100/(body\ length\text{‹}\ cm)^3$$

Where N_t was the number of fish in each cage at the end of this experiment and N_0 was the number of fish in each cage at the beginning of this experiment.

Where W_t was the final wet body weight (g), W_0 was the initial wet body weight and d was the experimental period in days.

One-way ANOVA was used for data statistics (SPSS 25.0, IBM, United States), and Tukey test was used for significance comparison between groups. Before Tukey's multiple range test, data were examined for normality and homogeneity of variances. Polynomial contrasts analysis was also performed in the pattern of linear and quadratic. $P < 0.05$ indicated significant difference. All results were expressed as the mean ± SEM.

3 Results

3.1 Survival, growth performance and body index

No significant differences were observed in survival rate, final weight, specific growth rate, feed intake, hepatosomatic index, viscerasomatic index, and condition factor among different dietary treatments ($P > 0.05$), but specific growth rate showed quadratic pattern with supplemental mixed bile acids (BA) level, peaking at fish fed diets supplemented with 600 mg/kg (Table 3). Compared with fish fed diets with SO, FCR of those fed diets supplemented with 600 mg/kg BA was significantly improved ($P < 0.05$).

3.2 Whole body proximate composition and muscle TG content

Whole body proximate composition and muscle TG content of juvenile large yellow croaker are shown in Table 4. In terms of whole body proximate composition, no significant differences were observed in moisture, crude protein, crude fat, and crude ash among different dietary treatments ($P > 0.05$), but moisture exerted a decreasing trend in linear pattern with the increase of supplemental BA level. Muscle TG content was linearly increased with the increase of dietary BA level ($P < 0.05$), and significant differences occurred as compared with fish fed diets with SO when supplemental BA level were reached 600 mg/kg and 1200 mg/kg ($P < 0.05$), respectively.

3.3 Skin color

Skin color of juvenile large yellow croaker is shown in Table 5. No significant differences were observed in the lightness (L*) of dorsal, lateral line, and abdominal skin among different dietary treatments ($P > 0.05$). The b* of dorsal skin showed no significant difference among different dietary treatments. The redness (a*) of dorsal and lateral line skin and the b* of abdominal skin showed significantly quadratic pattern with the increase of supplemental BA level ($P < 0.05$), peaking at fish fed diets supplemented with 600 mg/kg. The b* of lateral line skin was significantly linearly decreased with the increase of supplemental BA level ($P < 0.05$), and significant differences occurred in fish fed diets supplemented with 600 mg/kg and 1200 mg/kg BA compared with those fed diets with SO ($P < 0.05$). The a* of abdominal skin showed both significantly linear and quadratic decreasing pattern with the increase of supplemental BA level ($P < 0.05$), and it was significantly higher in fish fed diets supplemented with 1200 mg/kg BA compared with those supplemented with 300 mg/kg or 600 mg/kg ($P < 0.05$).

3.4 Dorsal muscle texture

Muscle texture of juvenile large yellow croaker fed with different diets is shown in Table 6. No significant differences were observed in hardness, adhesiveness, chewiness, and resilience among different dietary treatments ($P > 0.05$). Springiness showed a significantly decreasing trend in significantly linear and quadratic pattern with the

TABLE 3 Survival, growth performance and body index of juvenile large yellow croaker in different treatments (Means ± SEM, n = 3)[1].

Index	SO	BA300	BA600	BA1200	P-value	Linear	Quadratic
Survival rate (SR)	0.82 ± 0.02	0.81 ± 0.02	0.83 ± 0.04	0.80 ± 0.04	0.897	0.867	0.709
Final weight (g)	25.41 ± 0.81	29.11 ± 2.51	31.12 ± 1.70	27.42 ± 0.71	0.156	0.297	0.051
Specific growth rate (SGR, % day^{-1})	1.10 ± 0.05	1.32 ± 0.14	1.44 ± 0.09	1.23 ± 0.04	0.144	0.256	0.049
Feed intake rate (FI, %)	3.43 ± 0.09	3.19 ± 0.16	3.19 ± 0.15	3.34 ± 0.11	0.507	0.655	0.169
Feed conversion ratio (FCR)	1.56 ± 0.06^{a}	1.39 ± 0.03^{ab}	1.28 ± 0.02^{b}	1.48 ± 0.04^{ab}	0.018	0.108	0.004
Hepatosomatic index (HSI, %)	1.48 ± 0.10	2.66 ± 0.60	1.91 ± 0.15	1.73 ± 0.27	0.165	0.990	0.083
Viscerasomatic index (VSI, %)	4.97 ± 0.39	5.66 ± 0.47	4.97 ± 0.14	4.93 ± 0.34	0.446	0.626	0.331
Condition factor (K, %)	1.21 ± 0.02	1.22 ± 0.04	1.19 ± 0.02	1.23 ± 0.03	0.843	0.774	0.626

[1]Data are expressed as means values with their standard errors. Mean values with different superscripts are significantly different as determined by Tukey's test ($P < 0.05$).

increase of supplemental BA level, bottoming at fish fed diets supplemented with 600 mg/kg. However, cohesiveness and gumminess were significantly linear increased with the increase of supplemental BA level ($P < 0.05$), and significant differences were found in the fish fed diets supplemented with 1200 mg/kg BA compared with those fed diets with SO and 300 mg/kg BA ($P < 0.05$).

3.5 Plasma metabolites

Effect of dietary BA on plasma metabolites of juvenile large yellow croaker is shown in Figure 1. The contents of plasma total bile acid (TBA), total cholesterol (TC), glucose (GLU), and total protein (TP) showed no statistical difference among all treatments (Figures 1A–D) ($P > 0.05$).

3.6 Digestive enzyme activities

Effects of dietary BA on main digestive enzyme activities in the intestine of juvenile large yellow croaker are shown in Figure 2. No significant differences were observed in lipase, amylase, and trypsin activities (Figures 2A–C) ($P > 0.05$).

TABLE 4 Body composition of juvenile large yellow croaker in different treatments (Means ± SEM, n = 3)[1].

	SO	BA300	BA600	BA1200	P-value	Linear	Quadratic
Moisture (%)	78.08 ± 0.40	78.23 ± 0.56	76.50 ± 1.05	75.32 ± 1.47	0.184	0.049	0.509
Crude protein (%)	13.43 ± 0.24	12.82 ± 0.35	13.07 ± 0.32	13.37 ± 0.64	0.709	0.961	0.301
Crude fat (%)	3.16 ± 0.48	3.85 ± 1.43	3.80 ± 1.19	4.11 ± 0.37	0.915	0.544	0.849
Crude ash (%)	3.93 ± 0.39	3.75 ± 1.08	5.00 ± 0.94	5.56 ± 0.53	0.367	0.119	0.652
Muscle TG (mmol/gprot)	0.13 ± 0.00^{b}	0.16 ± 0.00^{ab}	0.19 ± 0.00^{a}	0.2 ± 0.01^{a}	0.002	0.000	0.248

[1]Data are expressed as means values with their standard errors. Mean values with different superscripts are significantly different as determined by Tukey's test ($P < 0.05$).

TABLE 5 Skin color parameters of juvenile large yellow croaker in different treatments (Means ± SEM, n = 3)[1].

		SO	BA300	BA600	BA1200	P-value	Linear	Quadratic
	L*	75.46 ± 3.09	68.48 ± 2.62	76.81 ± 3.43	72.58 ± 3.92	0.292	0.984	0.677
dorsal skin	a*	-1.79 ± 0.27^{b}	-1.46 ± 0.84^{b}	1.68 ± 0.46^{a}	-1.81 ± 0.24^{b}	0.007	0.282	0.012
	b*	22.72 ± 1.74	18.95 ± 1.85	17.63 ± 1.47	17.07 ± 0.65	0.075	0.015	0.295
	L*	78.99 ± 1.30	80.89 ± 1.96	71.57 ± 2.54	71.41 ± 3.79	0.021	0.010	0.679
lateral line skin	a*	-0.79 ± 1.04^{b}	-1.83 ± 0.44^{b}	2.38 ± 0.48^{a}	-1.92 ± 0.08^{b}	0.005	0.799	0.042
	b*	17.83 ± 1.05^{a}	16.20 ± 0.90^{ab}	13.41 ± 0.80^{b}	14.29 ± 0.57^{b}	0.007	0.002	0.148
	L*	82.35 ± 2.79	85.74 ± 0.51	85.14 ± 1.47	83.28 ± 1.41	0.499	0.325	0.731
abdominal skin	a*	-5.97 ± 0.75^{ab}	-6.71 ± 0.33^{b}	-6.87 ± 0.37^{b}	-4.21 ± 0.30^{a}	0.009	0.039	0.004
	b*	31.02 ± 2.01^{bc}	39.36 ± 2.59^{ab}	43.29 ± 2.44^{a}	26.09 ± 2.03^{c}	0.000	0.326	0.000

[1]Data are expressed as means values with their standard errors. Mean values with different superscripts are significantly different as determined by Tukey's test ($P < 0.05$).

TABLE 6 Dorsal muscle texture of juvenile large yellow croaker in different treatments (Means ± SEM, n = 3)[1].

	SO	BA300	BA600	BA1200	P-value	Linear	Quadratic
Hardness (g)	257.74 ± 6.94	237.55 ± 14.15	247.19 ± 6.99	246.06 ± 8.82	0.562	0.574	0.354
Adhesiveness (g·sec)	-21.46 ± 3.22	-21.97 ± 0.75	-16.76 ± 0.18	-20.52 ± 2.07	0.299	0.385	0.430
Springiness	0.76 ± 0.01^{a}	0.75 ± 0.02^{a}	0.69 ± 0.00^{b}	0.74 ± 0.01^{ab}	0.007	0.023	0.033
Cohesiveness	0.26 ± 0.01^{b}	0.26 ± 0.00^{b}	0.29 ± 0.01^{ab}	0.30 ± 0.01^{a}	0.012	0.002	0.691
Gumminess	65.28 ± 1.81^{bc}	59.24 ± 0.91^{c}	74.25 ± 0.17^{ab}	78.50 ± 4.31^{a}	0.002	0.001	0.063
Chewiness	49.53 ± 1.36	44.96 ± 2.90	55.56 ± 4.04	55.24 ± 1.71	0.071	0.052	0.457
Resilience	0.08 ± 0.01	0.07 ± 0.00	0.09 ± 0.01	0.09 ± 0.01	0.151	0.161	0.663

[1]Data are expressed as means values with their standard errors. Mean values with different superscripts are significantly different as determined by Tukey's test ($P < 0.05$).

3.7 Muscle fatty acids profiles

Fatty acids profile in the muscle of large yellow croaker is measured using a HP6890 gas chromatograph (Table 7). Muscle fatty acids profile showed no statistical difference among all treatments ($P > 0.05$). However, Total proportion of n-3LCPUFA showed a linearly increasing trend with the increase of supplemental BA level.

3.8 Real-time quantitative polymerase chain reaction

Gene expression of *cd36*, *fas*, *scd*, and *cpt1* showed no statistical difference among all treatments (Figures 3A–D) ($P > 0.05$). However, gene expression of *aco* was significantly decreased in fish fed diets supplemented with 600 mg/kg BA compared with 300 mg/kg other than those fed diets with SO (Figure 3E) ($P < 0.05$).

4 Discussion

In the present study, feed conversion rate (FCR) was significantly improved with the supplementation of mixed bile acids (BA) compared with fish fed diets with soybean oil (SO). The optimum dosage was 600 mg/kg and not in agreement with a previous finding in juvenile large yellow croaker (optimum dosage: 300 mg/kg) (Du et al., 2017; Ding et al., 2020). This discrepancy might be attributed to the differences of feed formations or ingredients of bile acids. It was reported that dietary bile acids could effectively increase feed utilization (Yamamoto et al., 2007; Jiang et al., 2018) and improve the growth performance of fish including largemouth bass (*Micropterus salmoides*) (Yu et al., 2019), rainbow trout (*Oncorhynchus mykiss*) (Yamamoto et al., 2007), and large yellow croaker (*Larimichthys crocea*) (Du et al., 2017). The reason why bile acids are important in improving FCR is that it can effectively improve the emulsification and transportation of lipids (Romanski, 2007).

Lipase activity can be recognized as an indicator of lipid utilization for animals. Previous studies showed dietary bile acids supplementation improved lipase activity as described in European eels (Zhai et al., 2020), rainbow trout (Adhami et al., 2017), large yellow croker (Ding et al., 2020), tilapia (Jiang et al., 2018), tongue sole (Li et al., 2021b), prenant's schizothoracin (Zeng et al., 2016; Xiang et al., 2019). Generally, bile acids are composed of a convex hydrophobic face and a concave hydrophilic face, this amphipathic structure is facilitated to lipid emulsification and breaks down large lipid molecules into small globules (Jiang et al., 2018), which provides lipase a higher surface area to digest lipids by catalyzing the hydrolysis of ester bonds (Romano et al., 2020). However, in this study, although lipase activity showed an upward trend, the difference was not significant. So we could attribute the improving FCR to the promoting emulsification of exogenous bile acids.

From the perspective of mixed bile acids, the main compositions are HDCA and CDCA. However, these components have seldom been studied in aquatic animals. Liao et al. (2020) reported that dietary bile acid (HDCA=69.9%) supplementation did not affect the growth performance of juvenile tiger puffer fed normal or high-lipid diets. Yin et al. (2021) found that dietary CDCA attenuated the adverse effects induced by high-fat diet on growth performance of largemouth bass, they attributed it to improving intestinal health, which conduced to the absorption and utilization of lipids. Du et al. (2017) reported that growth was significantly increased by dietary CDCA supplementation in large yellow croaker fed a soybean oil diet, they speculated that dietary CDCA might improve the growth performance by reducing inflammatory and improving health. Further studies are needed to explore the underlying mechanisms.

In addition to the improving feed conversion ratio, bile acids could also improve skin color and flesh quality of large yellow croaker in this study. Skin color is adopted as an index for assessing the quality of large yellow croaker, because it can directly affect the purchase of customers (Jiang et al., 2021). In this study, compared with fish fed diets with SO, supplementation of 600 mg/kg BA can significantly improve the redness (a*) of dorsal skin and the a* of lateral line skin. As a kind of fish characterized by yellow skin, the increase of skin color, especially yellowness (b*) of abdominal skin of large yellow croaker would improve commercial value. Moreover, muscle texture is also an important index for assessing the flesh quality of large yellow croaker. In the present study, the springness was decreased in fish

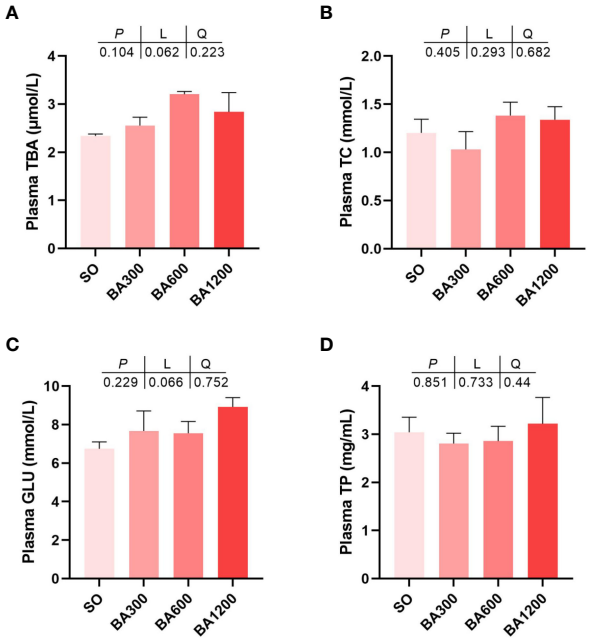

FIGURE 1
Plasma metabolites of juvenile large yellow croaker in different treatments. **(A)**, Plasma TBA; **(B)**, Plasma TC; **(C)**, Plasma GLU; **(D)**, Plasma TP. TBA, total bile acid; TC, total cholesterol; GLU, glucose; TP, total protein. Values are represented as mean ± SEM (n = 3).

fed diets supplemented with BA compared with those fed diets with SO. The reason should be attributed to the increase of triglyceride in muscle, this was in consistent with previous study in largemouth bass (Geng et al., 2018). Meanwhile, the increase of cohesiveness and gumminess could contribute to chewiness, suggesting that the taste of fish muscle was more tender, palatable and not sticky. As to the reason for the improvement of skin color and muscle texture, it was speculated that bile acids promoted the absorption of lipids and lipid-soluble substances such as pigments (Insull, 2006; Islam et al., 2011; Yang et al., 2022). This process was achieved through solubilizing dietary lipids and lipid-soluble substances as micelle by bile acids to facilitate their easily diffuse across the intestinal mucosa (de Aguiar Vallim et al., 2013). Synthesis and catabolism of triglyceride are very pivotal for lipid accumulation in a specific tissue (Li et al., 2013). The present study found that triglyceride (TG) content in muscle was markedly increased when supplemented 600 mg/kg and 1200 mg/kg bile acids. Similarly, previous studies have verified that dietary bile acids play an important role in regulating triglyceride metabolism (Ding et al., 2020). Consequently, we examined the gene expression related to fat metabolism in muscle. ACO is a key enzyme of fatty

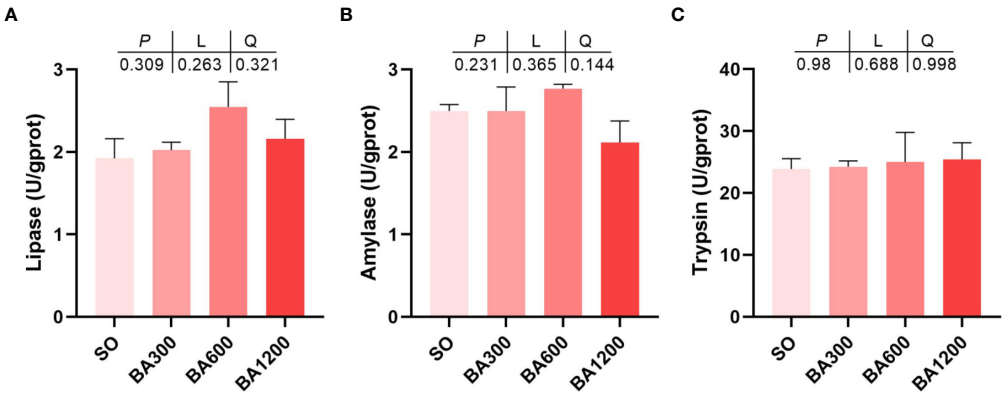

FIGURE 2
Activities of main digestive enzymes in the intestine of juvenile large yellow croaker in different treatments. **(A)**, Lipase; **(B)**, Amylase; **(C)**, Trypsin. Values are represented as mean ± SEM (n = 3).

TABLE 7 Fatty acids profile (% total fatty acids) in muscles of juvenile large yellow croaker in different treatments.

Fatty acids	SO	BA300	BA600	BA1200	P-value	Linear	Quadratic
C14:00	1.42 ± 0.19	1.11 ± 0.16	0.90 ± 0.05	1.19 ± 0.21	0.239	0.247	0.105
C16:00	19.42 ± 0.41	17.81 ± 0.92	17.73 ± 0.18	18.23 ± 0.44	0.198	0.181	0.094
C18:00	6.43 ± 0.61	6.45 ± 0.15	6.45 ± 0.22	6.57 ± 0.01	0.988	0.77	0.881
C20:00	0.42 ± 0.05	0.34 ± 0.03	0.36 ± 0.02	0.37 ± 0.03	0.405	0.398	0.191
∑SFA[1]	27.70 ± 0.37	25.69 ± 1.13	25.44 ± 0.19	26.36 ± 0.68	0.173	0.205	0.067
C16:1n-7	2.82 ± 0.39	2.40 ± 0.40	2.51 ± 0.35	2.50 ± 0.22	0.843	0.597	0.576
C18:1n-9	19.45 ± 1.25	21.59 ± 0.57	21.98 ± 0.78	20.80 ± 0.15	0.195	0.246	0.070
C24:1n-3	0.71 ± 0.17	0.36 ± 0.01	0.49 ± 0.13	0.53 ± 0.02	0.230	0.411	0.115
MUFA[2]	22.98 ± 1.01	24.35 ± 0.56	24.98 ± 1.03	23.82 ± 0.36	0.389	0.399	0.149
C18:2n-6	30.51 ± 0.14	32.26 ± 2.51	32.24 ± 0.61	31.28 ± 1.07	0.783	0.724	0.363
C20:2n-6	0.28 ± 0.13	0.49 ± 0.07	0.49 ± 0.07	0.54 ± 0.09	0.262	0.091	0.432
n-6PUFA[3]	30.79 ± 0.21	32.75 ± 2.53	32.72 ± 0.61	31.82 ± 1.16	0.745	0.645	0.348
C18:3n-3	4.44 ± 0.69	3.96 ± 0.10	3.95 ± 0.12	3.81 ± 0.13	0.635	0.269	0.643
C20:5n-3	1.59 ± 0.20	1.67 ± 0.19	1.83 ± 0.15	1.88 ± 0.03	0.557	0.182	0.934
C22:6n-3	3.27 ± 0.14	3.31 ± 0.08	3.80 ± 0.30	3.69 ± 0.10	0.154	0.057	0.683
n-3PUFA[4]	9.31 ± 0.95	8.94 ± 0.17	9.59 ± 0.21	9.39 ± 0.05	0.824	0.700	0.869
n-3PUFA/n-6PUFA[5]	0.30 ± 0.03	0.28 ± 0.03	0.29 ± 0.01	0.30 ± 0.01	0.865	0.978	0.540
n-3LCPUFA[6]	4.87 ± 0.33	4.98 ± 0.27	5.64 ± 0.15	5.58 ± 0.13	0.030	0.03	0.718
PUFA [7]	40.10 ± 1.16	41.69 ± 2.36	42.31 ± 0.74	41.21 ± 1.15	0.759	0.568	0.392

[1] SFA, saturated fatty acids.
[2] MUFA, mono-unsaturated fatty acids.
[3] n-6 PUFA, n-6 poly-unsaturated fatty acids.
[4] n-3 PUFA, n-3 poly-unsaturated fatty acids.
[5] n-3PUFA/n-6PUFA, the ratio of n-3 poly-unsaturated fatty acids to n-6 poly-unsaturated fatty acids.
[6] n-3 LC-PUFA, n-3 long chain poly-unsaturated fatty acids.
[7] PUFA, poly-unsaturated fatty acids.

acid oxidation, the gene expression level of *aco* in muscle of fish fed diets 600 mg/kg BA was down-regulated in the present study. Therefore, we inferred that supplemented dietary bile acids enhanced TG deposit in muscle by inhibiting fatty acids oxidation, and thereby improve the flesh quality of large yellow croaker. Inclusion of bile acids could activate FXR (Du et al., 2017). FXR plays a central role in the regulation of bile acid synthesis, excretion and transport (Chiang, 2009), and *fxr* expression has been reported to reduce bile acids synthesis by inhibiting the expression of *cyp7α1* in the liver (Zhou et al., 2018). Moreover, the activation of FXR could improve *pparα* expression and promote the β-oxidation of fatty acids (Xu et al., 2014). Therefore, in this study, the reason for lack of significant change in total bile acids (TBA) levels could be due to the down-regulation of *cyp7a1* expression and up-regulation of *pparα* expression, resulting in a reduction of BA synthesis and increase of fatty acids oxidation.

The fatty acids profile of diets could affect the fatty acids composition of fish muscle, which was well documented for gilthead sea bream (Regost et al., 2003a; Grigorakis, 2007) and large yellow croaker (Li et al., 2018). The substitution of fish oil by vegetable oils affected the fatty acids composition of fish, leading to increase of n-6PUFA and decrease of n-3PUFA in muscle and affecting flesh quality (Mu et al., 2018), In present study, compared with fish fed diets with SO, the level of total n-3LCPUFA showed a linearly increasing trend with the increase of supplemental bile acids level, which was consistent with study in large yellow croaker (Ding et al., 2020). n-3LCPUFA, especially, DHA and EPA play very important role in improving immunity, decreasing the risk of cardiovascular disease (Li et al., 2017). Therefore, promoting the increase of n-3LCPUFA by dietary bile acids inclusion will be beneficial for health in human.

5 Conclusion

In summary, the results of the present study showed that dietary 600 mg/kg mixed bile acids supplementation could improve feed conversion ratio, skin color and muscle texture of juvenile large yellow croaker. These findings would contribute to the long-term sustainable development of large yellow croaker farming. We will

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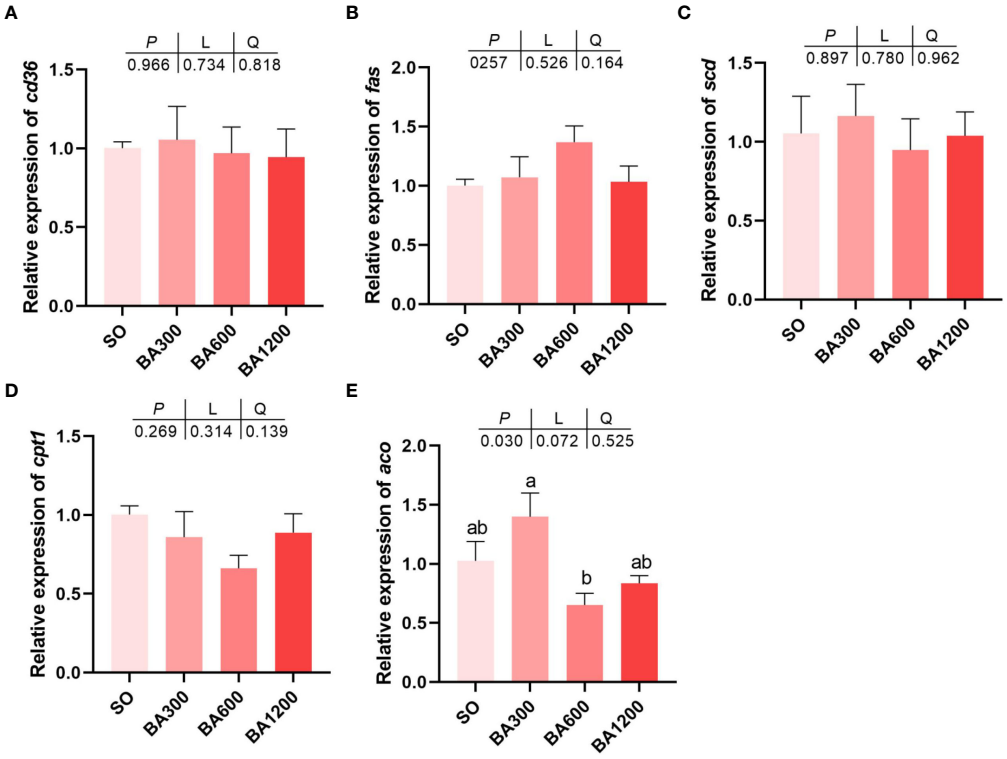

FIGURE 3
Gene expression of lipid metabolism **(A-E)** in the muscle of juvenile large yellow croaker in different treatments. Values are represented as mean ± SEM (n = 3). Bars with different lowercase letters represent significant difference ($P < 0.05$). *cd36*, cluster of differentiation 36; *fas*, fatty acid synthase; *scd*, stearoyl-coenzyme A desaturase; *cpt1*, carnitine palmitoyl transferase 1; *aco*, acyl-CoA oxidase.

intensively study the effects of bile acids on large yellow croaker through more comprehensive work such as adding fish oil group as control, increasing the quantity of sampled fish or selecting other different bile acids etc. in the future.

Data availability statement

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was reviewed and approved by Committee on the Ethics of Animal Experiments of Ocean University of China. Written informed consent was obtained from the owners for the participation of their animals in this study.

Author contributions

JL: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review and editing. ZW: Software, Methodology, Writing - review and editing. XC: Formal analysis, Methodology, Writing - review and editing. JW: Writing - review and editing. YG: Software, Methodology. XW: Software, Methodology. WL: Writing - review and editing. XB: Writing - review and editing. JZ: Writing - review and editing. KM: Supervision. QA: Conceptualization, Funding acquisition, Supervision, Writing - review and editing. All authors contributed to the article and approved the submitted version.

Funding

This research was financially supported by Scientific and Technological Innovation of Blue Granary with grant number (2019YFD0900202), the China Agriculture Research System (CARS47-11) and Leading Talent of Technological Innovation of Ten-Thousands Talents Program (CS31117200001).

Acknowledgments

We thank Jie Xue and Miao Weng for their help in diet preparation and the sample collection.

Conflict of interest

Author JW was employed by Shandong Longchang Animal Health Product Co., Ltd.

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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