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Dietary Lauric Acid Supplementation Positively Affects Growth Performance, Oxidative and Immune Status of European Seabass Juveniles

Filipa Fontinha [1,2,*], Nicole Martins [1,2], Rui Magalhães [1,2], Helena Peres [1,2] and Aires Oliva-Teles [1,2]

[1] Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), University of Porto, Terminal de Cruzeiros do Porto de Leixões, Av, General Norton de Matos s/n, 4450-208 Matosinhos, Portugal; rmagalhaes@ciimar.up.pt (R.M.); pereshelena@fc.up.pt (H.P.); up201829@up.pt (A.O.-T.)

[2] Departamento de Biologia, Faculdade de Ciências, University of Porto, Rua do Campo Alegre s/n, Ed. FC4, 4169-007 Porto, Portugal

* Correspondence: filipafontinha@hotmail.com

Abstract: Lauric acid (LA), a medium-chain fatty acid (C12), can promote growth performance and decrease oxidative damage and lipid deposition in animals. This study aimed to evaluate the effect of dietary supplementation of lauric acid as a functional ingredient on European seabass juveniles' growth performance and intestine antioxidant and immunological status. For this purpose, four practical diets were formulated to be isoproteic and isolipidic, including 0, 0.5, 1, and 2% of LA, and fed to triplicate groups of European seabass juveniles (~12.7 g) for 61 days. Dietary LA supplementation did not affect growth performance, feed utilization, or whole-body composition, but feed intake increased at a concentration-dependent level. However, the plasmatic triglyceride content was increased at the higher level of LA supplementation. In the intestine, catalase and glutathione reductase activities and lipid peroxidation levels were lower in fish fed the 1% LA diet than in the control group. The hepatic LPO level was higher in fish fed 0.5% LA than in the control group. Fish fed the 1% LA diet presented lower intestinal expressions of caspase 3, tumor necrosis factor-alpha, interleukins *10*, *6*, and *1-β*, and a lower plasma white blood cell number. Overall, up to 2% dietary supplementation of lauric acid as a functional ingredient showed a trend to improve European sea bass juveniles' growth performance without affecting feed utilization. Moreover, 1% dietary inclusion of LA reduced intestinal lipid peroxidation and downregulated pro-inflammatory and anti-inflammatory genes, thus enhancing the intestine's homeostatic status.

Keywords: medium-chain fatty acids; lauric acid; aquafeeds; welfare; immune response; European seabass

Key Contribution: The results further support the potential of lauric acid as a functional ingredient in aquafeeds, highlighting its dual role as a growth-promoting and immunostimulatory additive.

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1. Introduction

Aquaculture and fisheries production reached an all-time output of 223.2 million tonnes in 2022, contributing 20.7 kg of aquatic animal foods per capita [1]. Aquaculture production has increased by 6.6% since 2020, accounting for more than 57% of aquatic animal products directed to human consumption [1]. One of the downsides of increased fish production is rearing intensification, which can lead to economic losses due to higher fish

stress levels, decreased immunity, and lower ability to cope with pathogens, particularly in the early production stages.

Nutritional strategies show great potential to cope with these inconveniences, and efforts have been made to unlock the link between nutrition, welfare, immune response, and disease resistance [2].

One potential nutritional strategy is using medium-chain fatty acids (MCFAs) as functional ingredients. MCFAs include fatty acids with 8 to 12 carbon atoms, such as caprylic acid (C8), capric acid (C10), and lauric acid (C12). The primary sources of MCFAs are coconut and palm kernel oils, milk, and oil fractions of several plants [3,4]. They are extensively used in livestock diets as a source of easily accessible energy [4–6]. Since they are more polar than long-chain fatty acids and less reliant on chylomicrons and lipoproteins for transport, they can be readily absorbed by enterocytes [7,8]. Moreover, MCFA consumption has been related to decreased feed intake and reduced fat deposition, improved growth performance, disease resistance, and immunity in mammals [7,9].

The beneficial effects of dietary MCFAs were also demonstrated in fish. For instance, in gilthead sea bream (*Sparus aurata*), supplementation with 0.3% sodium salt of coconut fatty acid distillate rich in lauric acid (LA) was shown to enhance feed intake, improve nutrient absorption and growth rate, and upregulate the expression of immune-related genes [10]. In Nile tilapia (*Oreochromis niloticus*), diets containing increasing levels of MCFA from palm oil promoted increased weight gain, feed efficiency, and protein efficiency ratio [11].

Lauric acid (LA) is an MCFA primarily found in coconut and palm oils, making up 45.5% and 46.1% of the total fatty acids. It is a potent antimicrobial agent, suggesting that it has the potential to be used as a strategy for mitigating the use of antibiotics in animal farming [12]. In chicken, dietary LA supplementation was shown to increase the weight gain, intestinal morphology, serum total protein, and antioxidant capacity of yellow-feathered broilers [13]. No differences in growth performance or serum biochemical parameters were observed in broiler chickens fed a blend with 4% capric acid, lauric acid, and coconut oil [14]. In fish, LA supplementation has been demonstrated to improve growth performance and feed efficiency in zebrafish (*Danio rerio*) [15]. Similarly, in black sea bream (*Acanthopagrus schlegelii*), LA-enriched diets led to increased growth performance, improved feed utilization, enhanced intestinal histomorphology, and reductions in plasma triglyceride levels and lipid peroxidation [8].

European seabass is a marine fish species of considerable economic significance in European aquaculture, renowned for its high-quality flesh, adaptability to farming environments, and substantial consumer demand. Its rapid growth, robustness, and market value position it as a key subject of research in the fields of fish nutrition, health, and sustainable aquaculture practices. This study evaluated the incorporation of LA as a functional ingredient in the diets of European seabass juveniles, focusing on its effects on growth performance, plasma metabolites, antioxidant activity, and immune parameters.

2. Material and Methods

2.1. Experimental Diets

Four practical diets were formulated to be isoproteic (45% crude protein) and isolipidic (19% crude lipid) and to include graded levels of lauric acid (0, 0.5, 1, and 2%) (Table 1). Lauric acid (Alfa Aesar A11672.36) was mixed with fish and colza oil before being added to the diets. All ingredients were enterally mixed and pelletized using a laboratory pellet mill (California Pellet Mill, CPM Crawfordsville, IN, USA) with a 3 mm die. The pellets were subsequently dried in an oven at 50 °C for 48 h and stored at −20 °C until use.

Table 1. Ingredients and proximate composition of the experimental diets.

Diets				
Ingredients (% Dry Matter)				
	0LA	**0.5LA**	**1LA**	**2LA**
Fish meal [1]	15.0	15.0	15.0	15.0
Hydrolized salmon [2]	2.00	2.00	2.00	2.00
Soybean meal [3]	20.0	20.0	20.0	20.0
Corn gluten [4]	17.5	17.5	17.5	17.5
Wheat gluten [5]	9.69	9.69	9.69	9.69
Rapeseed [6]	5.00	5.00	5.00	5.00
Wheat meal [7]	8.20	8.20	8.20	8.20
Fish oil	7.98	7.98	7.98	7.98
Colza oil	7.98	7.98	7.98	7.98
Vitamin [8]	1.00	1.00	1.00	1.00
Choline [9]	0.50	0.50	0.50	0.50
Mineral [10]	1.00	1.00	1.00	1.00
Binder [11]	1.00	1.00	1.00	1.00
Dicalcium phosphate	0.66	0.66	0.66	0.66
Methionine [12]	0.17	0.17	0.17	0.17
Taurine [13]	0.30	0.30	0.30	0.30
Cellulose	2.00	1.50	1.00	0.00
Lauric acid [14]	0.00	0.50	1.00	2.00
Proximate composition (% dry matter)				
Dry Matter (DM %)	90.5	90.8	90.9	90.7
Crude Protein	45.7	45.1	45.7	45.8
Crude Lipids	18.6	19.3	18.7	18.6
Ash	7.83	8.03	8.21	7.78

LA—Lauric acid, [1] Sorgal, S.A. Ovar, Portugal (CP: 66.2% DM; CL: 7.42% DM). [2] Sorgal, S.A. Ovar, Portugal (CP: 30.0% FW; CL: 5.00% FW). [3] Sorgal, S.A. Ovar, Portugal (CP: 49.5% DM; CL: 1.47% DM). [4] Sorgal, S.A. Ovar, Portugal (CP: 72.8% DM; CL: 1.03% DM). [5] Sorgal, S.A. Ovar, Portugal (CP: 81.8% DM; CL: 1.52% DM). [6] Sorgal, S.A. Ovar, Portugal (CP: 39.5% DM; CL: 0.81% DM). [7] Sorgal, S.A. Ovar, Portugal (CP: 10.8% DM; CL: 0.50% DM). [8] Vitamin premix (mg/kg diet): retinol, 18,000 (IU/kg diet); calciferol, 2000 (IU/kg diet); alpha-tocopherol, 35; menadione sodium bis., 10; thiamin, 15; riboflavin, 25; Ca pantothenate, 50; nicotinic acid, 200; pyridoxine, 5; folic acid, 10; cyanocobalamin, 0.02; biotin, 1.5; ascorbyl monophosphate, 50; inositol, 400. [9] Sorgal, S.A. Ovar, Portugal. [10] Minerals premix (mg/kg diet): cobalt sulfate, 1.91; copper sulfate, 19.6; iron sulfate, 200; sodium fluoride, 2.21; potassium iodide, 0.78; magnesium oxide, 830; manganese oxide, 26; sodium selenite, 0.66; zinc oxide, 37.5; dicalcium phosphate, 8.02 (g/kg diet); potassium chloride, 1.15 (g/kg diet); sodium chloride, 0.4 (g/kg diet). [11] Aquacube, Agil, UK. [12] Feed-grade methionine, Sorgal, S.A., Ovar, Portugal. [13] Feed-grade taurine, Sorgal, S.A., Ovar, Portugal. [14] Feed-grade lauric acid, Alfa Aesar A11672.36.

2.2. Growth Trial

The growth trial was conducted at CIIMAR facilities by skilled researchers (following FELASA category C guidelines), in compliance with the European Union Directive (2010/63/EU).

All animals were maintained according to the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines, ensuring ethical standards in animal research. The procedures were authorized by the ORBEA Animal Welfare Committee at CIIMAR (reference ORBEA_CIIMAR_27_2019), adhering to the European Union directive 2010/63/EU and the Portuguese legislation DL 113/2013.

European seabass juveniles were obtained from Atlantik Fish, Lda. in Castro Marim, Portugal, and transported to the research facility, where they underwent a 15-day quarantine period. During this period, fish were fed with a commercial diet and the water environmental parameters were the same as those in the growth trial. Following this, the fish were relocated to the experimental system, featuring two identical recirculating aquaculture systems (RASs). Each system was equipped with 12 cylindrical fiberglass tanks,

each holding 250 L. Water from the tanks passed through a mechanical filter, followed by a biological filter, and then a sand filter before being cycled back into the tanks.

After a 15-day acclimatization period, 12 uniform groups of 30 fish (total fish 360), each with an initial weight of approximately 12.7 g, were randomly distributed to the experimental tanks. Diets were randomly allocated into triplicate groups, and fish were hand-fed twice daily (at 9:30 and 15:30) for six days a week until apparent visual satiety. The trial lasted 61 days, with water temperature maintained at 22 ± 1 °C, dissolved oxygen levels above 80%, a photoperiod of 12 h light and 12 h dark, salinity at 26 ± 1‰, and nitrogenous compounds kept below 0.02 mg/L.

2.3. Sampling

At the end of the growth trial, fish were not fed for 24 h before being weighed collectively. Three fish from each tank were euthanized with an overdose of 2-phenoxyethanol (1 mL/L), and the individual wet weight, liver, and viscera weights were recorded to determine hepatosomatic (HSI) and viscerosomatic indices (VSI). Then, the whole fish was stored at −20 °C until whole-body composition determination. Ten fish from the initial stock were also euthanized at the beginning of the growth trial as described above and stored at −20 °C for whole-body composition determination.

To minimize handling stress, the remaining fish were fed for an additional 3 days before sampling. Four hours following the morning meal, 3 fish per tank (9 per treatment) were randomly selected. Blood samples were obtained from the caudal vein using syringes treated with heparin and divided into two aliquots: one for total white (WBC) and red blood (RBC) cell counts, and the other was centrifuged at 10,000× *g* for 10 min at 4 °C and plasma was stored at −20 °C for blood parameter analysis. Following blood collection, fish were euthanized by decapitation. After that, the liver and anterior intestine were removed and promptly kept at −80 °C for further examination of lipid peroxidation, gene expression, and antioxidant enzyme activity.

2.4. Chemical Analysis

The chemical composition of ingredients, diets, and whole fish was assessed according to the methods established by the Association of Official Analytical Chemists [16]. Dry matter content was measured by drying samples at 105 °C in an oven until a constant weight was reached. Ash content was determined by incinerating samples in a muffle at 450 °C for 16 h. Total protein content, expressed as N × 6.25, was assessed using the Kjeldahl method after acid digestion, employing a Kjeltec digestion and distillation system (Tecator Systems, Höganäs, Sweden; models 1015 and 1026, respectively). The total lipid content was quantified through petroleum ether extraction using a Soxtec extraction system (Tecator Systems, Höganäs, Sweden; extraction unit model 1043 and service unit model 1046).

2.5. Plasmatic Metabolites

Commercial kits from Spinreact, S.A. (Gerona, Spain) were used to determine the plasma glucose (cod. 1001191), triglycerides (TAG; cod. 1001312), total cholesterol (cod. 1001092), and total proteins (cod. 1001290). The plasma parameters were assessed through colorimetric assays, and the absorbance values were recorded using a Multiskan GO microplate reader (Model 5111 9200; Thermo Scientific, Nanjing, China).

2.6. Hematological Parameters

The RBC and WBC count were conducted according to [17] Fontinha et al. (2024). Hematocrit levels were assessed after spinning the samples at 10,000× *g* for 10 min at room temperature. Hemoglobin levels were quantified using a commercial kit (Spinreact, S.A.; cod. 1001230, Barcelona, Spain). The mean corpuscular volume (MCV), mean corpuscu-

lar hemoglobin (MCH), and mean corpuscular hemoglobin concentration (MCHC) were derived using standard calculations.

2.7. Enzyme Activity and Lipid Peroxidation

After weighing and homogenizing (dilution 1:5) the liver and intestinal samples in 100 mM Tris-HCL buffer with 0.1 mM EDTA and 0.1% Triton X-100, pH 7.8, they were centrifuged at 30,000× *g* for 30 min at 4 °C. Before being used, the supernatants were separated into aliquots and kept at −80 °C. All enzymes were determined at 37 °C, and absorbances were read.

Catalase (CAT, EC 1.11.1.6) was determined according to Aebi [18]; glutathione peroxidase (GPX, EC 1.11.1.9) as described by Flohé and Günzler [19]; glutathione reductase (GR, EC 1.6.4.2) according to Morales et al. [20]; and protein was quantified according to Bradford [21], using a kit (cod. 5.000.006).

Enzyme activities are presented as units (CAT) or mili-units (GPX and GR) per milligram of soluble protein. The quantity of enzyme required to catalyze the transformation of 1 µmol of the substrate per minute is known as one enzyme unit. According to Buege and Aust (1978) [22]. the degree of lipid peroxidation (LPO) was estimated by malondialdehyde (MDA) measurement, which is given as nmol MDA/g tissue.

2.8. Gene Expression

RNA was extracted from each sample utilizing a Precellys evolution homogenizer (Bertin Instruments, Montigny-le-Bretonneux, France) and the TRIzol reagent (Direct-zol™ RNA Miniprep, Zymo Research, Irvine, CA, USA), following the protocols provided by the manufacturer.

The RNA concentration was verified using spectrophotometry (µDropTM plate, ThermoScientific, Waltham, VA, USA), and its integrity was evaluated through electrophoresis on a 1% agarose gel. The RNA was then diluted to a concentration of 0.5 µg/8 µL in water for the synthesis of complementary DNA, which was carried out using the NZY First-Strand cDNA Synthesis Kit (NZYTech, MB12502, Lisbon, Portugal).

Gene expression levels in the anterior intestine were assessed using real-time quantitative PCR (CFX Connect™ Real-Time System, Bio-Rad, Hercules, CA, USA). Primer sequences were obtained in the genbank database. Primer efficiency was confirmed through serial two-fold dilutions of cDNA, with calculations based on the slope of the quantification cycle (Ct) regression line plotted against the relative cDNA concentration. NF-kβ primer sequences were sourced from the European seabass genome database (http://seabass.mpipz.mpg.de/cgi-bin/hgGateway) (accessed on 1 September 2024). The reference genes *ef1α* and *40s* were used to normalize our qPCR data (Table 2). To ensure accurate and reliable quantification, we employed the geometric mean of their Ct values.

Table 2. Primer sequences utilized for real-time quantitative PCR analysis to assess immune-related gene expression.

Gene	Accession Number	Primer Efficiency	Annealing Temperature	Primer Forward	Primer Reverse
ef1α	AJ866727	1.96	63 °C	GCTTCGAGGAAATCACCAAG	CAACCTTCCATCCCTTGAAC
40s	HE978789.1	1.90	63 °C	TGATTGTGACAGACCCTCGTG	CACAGAGCAATGGTGGGGAT
tnf-α	DQ200910	1.90	63 °C	AGCCACAGGATCTGGAGCTA	GTCCGCTTCTGTAGCTGTCC
il-10	AM268529	1.93	63 °C	ACCCCGTTCGCTTGCCA	ATCTGGTGACATCACTC
tgf-β	AM421619.1	1.88	63 °C	GACCTGGGATGGAAGTGGAT	CAGCTGCTCCACCTTGTGTTG
il-1β	AJ311925.1	2.05	63 °C	ATCTGGAGGTGGTGGACAAA	AGGGTGCTGATGTTCAAACC
nf-kβ	DLAgn_00239840	1.90	63 °C	GCTGCGAGAAGAGAGGAAGA	GGTGAACTTTAACCGGACGA
casp3	DQ345773	2.08	63 °C	CTGATTTGGATCCAGGCATT	CGGTCGTAGTGTTCCTCCAT

ef1α—Elongation factor *1α*; *40s*—Ribosomal protein S40; *tnf-α*—Tumor necrosis factor-α; *il-10*—Interleukin 10; *tgf-β*—Transforming growth factor- β; *il-1β*—Interleukin 1 β; *nf-kβ*—Nuclear factor kappa β; *casp3*—Caspase 3.

2.9. Statistic Analysis

The data are presented using the mean and pooled standard error of the mean (SEM). Statistical significance was determined at a probability level of 0.05, leading to the rejection of the null hypotheses. Normality and homogeneity of variances were assessed using the Shapiro–Wilk and Levene tests, respectively, with normalization applied where necessary. The analysis was conducted using polynomial contrasts and one-way ANOVA. All statistical evaluations were performed using the SPSS 28.0 software for Windows (IBM® SPSS® Statistics, Armonk, NY, USA).

3. Results

3.1. Growth Performance and Whole-Body Composition

The fish readily adapted to the provided diets, and the mortality rate throughout the trial remained minimal, with no correlation to the specific experimental diets. Feed intake (FI) linearly increased with dietary LA supplementation and was significantly higher in fish fed the 2LA diet than in the control (Table 3). Growth performance and feed utilization, expressed as final body weight, weight gain, daily growth index, feed efficiency, and protein efficiency ratio, were not affected by the different dietary levels of LA.

Table 3. Growth performance and feed utilization efficiency of European sea bass fed the experimental diets.

	Diets					Polynomial Contrasts		
	0LA	0.5LA	1LA	2LA	SEM	ANOVA	Linear	Quadratic
Initial body weight (g)	12.7	12.7	12.7	12.7	0.01	0.25	0.85	0.07
Final body weight (g)	33.8	33.0	35.4	35.4	1.79	0.17	0.08	0.60
Weight gain (g/Kg ABW/day) [1]	14.9	14.6	15.5	15.5	0.14	0.17	0.08	0.56
Daily Growth Index [2]	1.48	1.44	1.56	1.56	0.02	0.17	0.08	0.58
Feed Intake (g/Kg ABW/day) [3]	18.6 [a]	19.3 [ab]	19.6 [ab]	20.3 [b]	0.15	0.02	0.00	0.96
Feed Efficiency [4]	0.80	0.76	0.79	0.77	0.01	0.52	0.44	0.71
Protein Efficiency Ratio [5]	1.76	1.68	1.73	1.67	0.02	0.62	0.35	0.84
N Retention (% N intake) [6]	22.2	19.9	21.5	23.0	0.62	0.34	0.47	0.14
Survival (%)	100	98.9	100	100	0.18	0.44	0.67	0.35

LA—Lauric acid. Values are presented as means (n = 3). SEM: pooled standard error of the mean. Means in the same row with different superscript letters are significantly different (Tukey test; $p < 0.05$). Average body weight (ABW): initial body weight (IBW) + final body weight (FBW)/2. [1] Weight gain, % = [(Final weight − Initial weight)/Initial weight] × 100. [2] DGI = [(Final weight1/3 − Initial weight1/3)/time in days] × 100. [3] FI = Total dry feed intake/Average body weight/days. [4] FE = wet weight gain/dry feed intake. [5] PER = weight gain/crude protein intake. [6] N Retention (% N intake) = (Nitrogen retention (g/kg ABW/day)/Nitrogen intake) × 100.

The experimental diets did not affect the final whole-body composition (Table 3). The hepatosomatic and visceral indexes were also not significantly affected by diet com-

position (Table 4). Nevertheless, there was a significant quadratic trend response for the visceral index.

Table 4. Whole-body composition (%wet weight), hepatosomatic, and visceral indices of European seabass juveniles fed the experimental diets.

		Diets					Polynomial Contrasts		
	Initial	**0LA**	**0.5LA**	**1LA**	**2LA**	**SEM**	**ANOVA**	**Linear**	**Quadratic**
Dry Matter	36.2	37.0	36.1	35.8	38.0	0.55	0.62	0.62	0.25
Protein	18.8	19.2	18.8	18.7	19.9	0.31	0.57	0.54	0.25
Lipids	10.0	12.2	12.1	12.0	12.5	0.19	0.84	0.66	0.48
Ash	9.40	5.70	6.20	6.30	5.70	0.18	0.48	0.93	0.14
VSI (%) [1]	-	10.4	9.32	8.83	10.9	0.32	0.09	0.74	0.02
HSI (%) [2]	-	1.26	1.23	1.10	1.28	0.04	0.45	0.81	0.22

LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. [1] Viscerosomatic index = (visceral weight/whole body weight) × 100. [2] Hepatosomatic index = (liver weight/whole body weight) × 100.

3.2. Plasmatic Metabolites

The diet composition did not affect plasma total proteins, glucose, or cholesterol (Table 5). However, plasma triglycerides linearly increased with dietary LA level and were considerably increased in fish fed the 2LA diet compared to the control.

Table 5. Plasmatic metabolites (mg/dL) of European seabass juveniles fed the experimental diets.

	Diets					Polynomial Contrasts		
	0LA	**0.5LA**	**1LA**	**2LA**	**SEM**	**ANOVA**	**Linear**	**Quadratic**
Total Proteins	1632	1643	1662	1577	50.7	0.95	0.76	0.65
Glucose	82.9	77.8	82.7	87.3	4.13	0.89	0.64	0.57
Cholesterol	53.2	48.7	56.5	58.9	1.85	0.13	0.08	0.27
Triglycerides	399 ^{a}	427 ^{ab}	528 ^{ab}	539 ^{b}	20.0	0.02	0.00	0.81

LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. Means in the same row with different superscript letters are significantly different (Tukey test; $p < 0.05$).

3.3. Hematological Parameters

No dietary effects were noted in the hematological parameters measured, except for WBC count, which was significantly lower in fish fed the 1LA diet than in the other LA-supplemented diets (Table 6). Furthermore, a linear trend for MCV to decrease with increased dietary LA supplementation was also observed (Table 6).

Table 6. Hematological parameters of European seabass juveniles fed the experimental diets.

	Diets					Polynomial Contrasts		
	0LA	**0.5LA**	**1LA**	**2LA**	**SEM**	**ANOVA**	**Linear**	**Quadratic**
WBC [1]	8.13 ^{ab}	9.06 ^{b}	6.98 ^{a}	9.66 ^{b}	0.27	0.00	0.22	0.06
RBC [2]	2.86	3.15	2.85	3.28	0.11	0.46	0.35	0.77
Hemoglobin [3]	1.69	1.92	1.55	1.65	0.12	0.74	0.65	0.79
Hematocrit [4]	32.9	31.6	28.8	30.3	1.06	0.59	0.70	0.30
MCH [5]	7.25	5.97	5.63	5.11	0.56	0.61	0.20	0.75
MCV [6]	126	102	101	87.8	6.28	0.06	0.01	0.99
MCHC [7]	5.40	5.96	5.67	5.30	0.39	0.95	0.84	0.84

LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. Means in the same row with different superscript letters are significantly different (Tukey test; $p < 0.05$). [1] White Blood Cells ($\times 10^4$/µL), [2] Red Blood Cells ($\times 10^6$/µL), [3] Hemoglobin (g/dL), [4] Hematocrit (%), [5] Mean Corpuscular Hemoglobin (pg/cell), [6] Mean Corpuscular Volume (µm^3), [7] Mean Corpuscular Hemoglobin Concentration (g 100/mL).

3.4. Oxidative Status

In the intestine, CAT and GR activities and LPO followed a significative negative quadratic function, with the minimum value observed in fish fed the 1LA diet (Table 7). GPX activity also followed a similar negative quadratic trend.

Table 7. Antioxidant enzyme activity and lipid peroxidation in the intestine of European sea bass fed experimental diets.

	Diets.					Polynomial Contrasts		
	0LA	**0.5LA**	**1LA**	**2LA**	**SEM**	**ANOVA**	**Linear**	**Quadratic**
CAT [1]	542 [b]	526 [ab]	379 [a]	424 [ab]	21.6	0.01	0.01	0.00
Gpx [2]	117	101	75.8	77.7	7.62	0.16	0.04	0.52
GR [3]	98.8 [b]	78.0 [ab]	65.9 [a]	78.4 [ab]	3.66	0.01	0.02	0.01
LPO [4]	90.2 [b]	65.2 [ab]	46.6 [a]	70.1 [ab]	5.19	0.00	0.01	0.00

LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. Means in the same row with different superscript letters are significantly different (Tukey test; $p < 0.05$). [1] Catalase (U/mg protein); [2] Glutathione peroxidase (mU/mg protein); [3] Glutathione reductase (mU/mg protein); [4] Lipid peroxidation (MDA/g tissue).

In the liver, diet composition did not significantly affect CAT, GR, or GPX activities (Table 8). Nevertheless, GPX activity followed a negative quadratic trend, with the minimum value being observed in fish fed the 1LA diet. On the other hand, diet composition significantly affected LPO levels, which were significantly higher in fish fed the 0.5LA diet than in the control.

Table 8. Antioxidant enzyme activity and peroxidation in the liver of European sea bass fed experimental diets.

	Diets					Polynomial Contrasts		
	0LA	**0.5LA**	**1LA**	**2LA**	**SEM**	**ANOVA**	**Linear**	**Quadratic**
CAT [1]	185	142	140	136	12.3	0.47	0.19	0.44
GPX [2]	16.5	11.7	11.3	19.2	1.2	0.06	0.47	0.01
GR [3]	1.85	3.32	2.18	3.25	0.25	0.08	0.16	0.68
LPO [4]	32.9 [a]	58.7 [b]	56.5 [ab]	37.4 [ab]	5.15	0.025	0.772	0.050

LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. Means in the same row with different superscript letters are significantly different (Tukey test; $p < 0.05$). [1] Catalase (U/mg protein); [2] Glutathione peroxidase (mU/mg protein); [3] Glutathione reductase (mU/mg protein); [4] Lipid peroxidation (MDA/g tissue).

3.5. Effects of LA Supplementation on Gene Expression

The relative expressions of *nf-kβ* and *tgf-β* in the anterior intestine were not affected by diet composition (Figure 1). However, the expressions of *tnf-α*, *il-1β*, *il-10*, and *casp3* exhibited a quadratic response, with the lowest expression being observed in fish fed the 1LA diet (Figure 1).

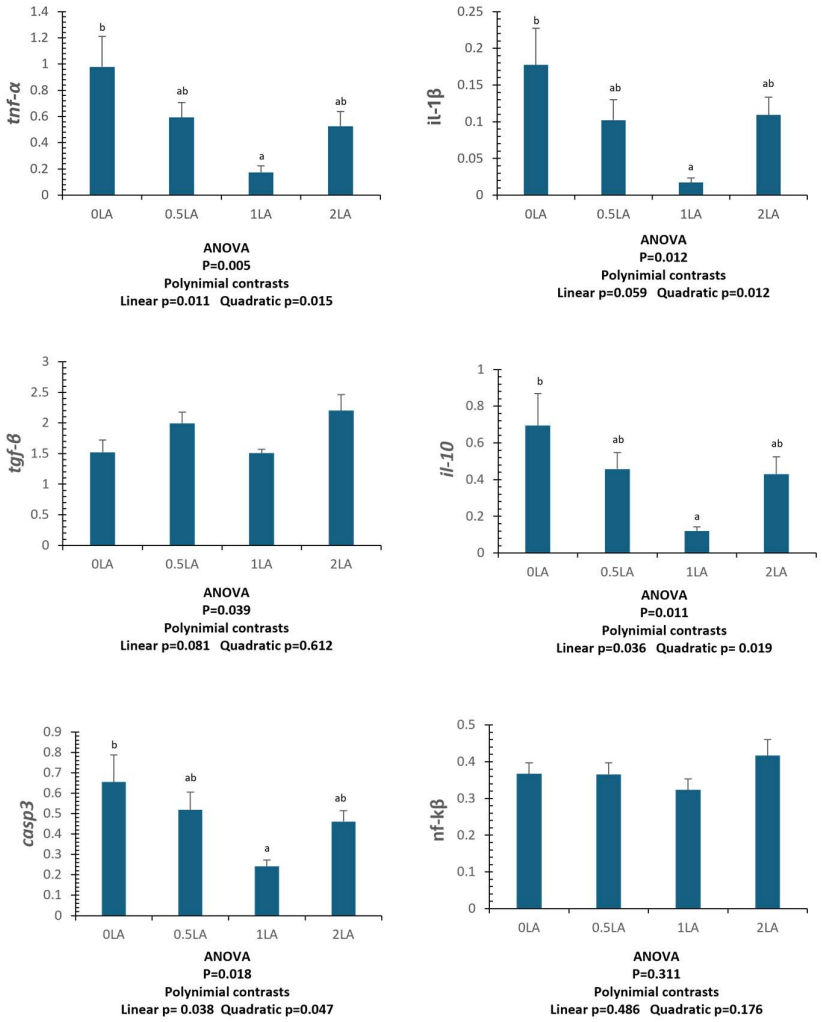

Figure 1. Relative gene expression of immune-related genes in the anterior intestine of European seabass juveniles fed experimental diets. LA—Lauric acid. Values are presented as mean (n = 9). SEM: pooled standard error of the mean. Superscript letters are significantly different (Tukey test; $p < 0.05$).

4. Discussion

Medium-chain fatty acids (MCFAs), such as lauric acid (LA), are rapidly absorbed by cells, efficiently utilized as an energy source, and can provide health benefits beyond basic nutrition [23]. As a nutritional supplement, MCFAs provide an energy-dense feed component that is promptly utilized by the cells as energy fuel. At the same time, their functional properties include antimicrobial effects and immune-boosting benefits, making them an appealing ingredient for aquafeeds [24]. Studies in fish have shown that LA also functions as an acidifier, lowering intestinal pH [4]. The decrease in pH levels aids in suppressing pathogens that are sensitive to acidity, while simultaneously promoting the proliferation of beneficial gut microorganisms. This supports enhanced gut health and contributes to overall well-being and performance.

In the present study, dietary supplementation with LA as a functional ingredient (up to 2%) led to a linear trend (p = 0.08) in increased growth rate and a significant increase (p = 0.02) in feed intake while not affecting feed efficiency. These findings align with prior research highlighting the benefits of MCFAs and their derivatives in aquaculture.

Common carp fed diets with high lipid levels and supplemented with glycerol monolaurate showed increased feed intake, final body weight, and feed efficiency [25]. Similarly, Nile tilapia fed with graded levels of alpha-monolaurin (2, 4, and 6 g/kg) achieved the highest growth and feed efficiency at the 6 g/kg inclusion level [6]. Also, a combination

of MCFAs (1, 2, and 3 g/kg) and taurine used as a digestive/metabolic enhancer (DME, AQUAGEST) enhanced the final weight, specific growth rate, and feed intake in common carp (*Cyprinus carpio*) in a dose-dependent manner [26]. Likewise, including 0.1% lauric acid (LA) in black sea bream diets enhanced specific growth rate, weight gain, final body weight, and feed efficiency compared to the control [8]. Similarly, the growth of tambaqui (*Colossoma macropomum*) fed with diets including increasing levels of coconut oil replacing soybean oil was maximized with the dietary inclusion of 50% coconut oil, corresponding to a dietary LA of 2.65%, without affecting feed utilization [27]. Further, gilthead sea bream fed with a diet including 0.3% coconut fatty acid distillate (DICOSAN®), which is rich in C-12, also showed increased growth performance while not affecting feed utilization [10].

Contrary to mammals, where MCFAs have been associated with enhanced satiety and reduced food intake [9], in the present study, dietary supplementation with LA led to a significant linear increase in feed intake. This was partially unexpected, as it was previously observed that European sea bass fed with diets including 12 to 24% lipids had the same feed intake [28,29], suggesting that dietary lipid level inefficiently regulates feed intake in this species. The increased feed intake observed in the present study indicates that LA may have acted as a feed stimulant, but further research is required to confirm this hypothesis.

The observed increase in feed intake is positively associated with elevated plasma cholesterol and triglyceride levels. In tambaqui, plasma triglyceride and cholesterol levels also increased with the dietary inclusion of coconut oil [27], and black seabream fed with diets enriched with 0.8% lauric acid also exhibited increased feed intake alongside higher plasma triglyceride levels [8]. Differently, common carp fed with high-lipid diets supplemented with GML exhibited reduced plasma triglyceride levels, while no significant differences were observed in total cholesterol levels [25]. Moreover, in gilthead sea bream fed with a diet including 0.3% coconut fatty acid distillate (DICOSAN®), plasma cholesterol and triglyceride levels were not affected [10]. While coconut oil is rich in LA, it also contains small amounts of other MCFAs, such as caprylic and capric acid, and long-chain saturated fatty acids like myristic and palmitic acid. Accordingly, results may not be solely attributable to the lauric acid content, underscoring the complexity of its effects [30].

Without adequate antioxidant defense, reactive oxygen species (ROS) can compromise cellular function, damaging vital cellular components such as lipids, proteins, and nucleic acids, ultimately resulting in stress-induced cell death [31]. Medium-chain fatty acids, particularly LA, have been shown to enhance the activity of key endogenous antioxidant enzyme activity, including superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPx) [25]. These enzymes play a crucial role in neutralizing oxidative stress by mitigating the harmful effects of ROS, thereby maintaining immune defense and protecting cellular integrity [32,33].

ROS plays a crucial role in regulating immune cells' proliferation, differentiation, and function. Neutrophils, essential components of the innate immune response, generate significant amounts of ROS upon activation to eliminate pathogens. Similarly, macrophages, which are involved in both innate and adaptive immune responses, are also influenced by ROS levels. The production of ROS in these immune cells is tightly regulated, as it not only aids in pathogen clearance but also affects the cells' survival and functional capacities [34].

There are not many studies evaluating the antioxidant potential of LA in fish. The results of the present study suggest a protective effect of dietary LA in the intestine, as evidenced by reduced lipid peroxidation (LPO) levels and antioxidant enzyme activity, which was particularly significant at a dietary supplementation of 1% LA. In black sea bream, dietary inclusion of 0.1% LA was also shown to have a protective effect by reducing serum LPO levels [8], while in gilthead sea bream, plasma antioxidant capacity (Trolox mM) remained unaltered by the dietary supplementation with 0.3% coconut fatty acid distillate

(DICOSAN®) [10]. Also, in the present study, LA did not contribute to improved LPO levels in the liver. On the contrary, LPO levels were higher in fish fed the 0.5LA and 1LA diets than in the control. GPX activity was also lower in fish fed with these diets, which contributes to explaining the increased LPO in these groups. Differently, in Nile tilapia, hepatic activities of SOD, CAT, and GPX were increased, and LPO levels decreased with dietary inclusion of alpha-monolaurin [6].

The intestine forms the first barrier against the entrance of pathogens and serves as a frontline in the immune system, and its health and integrity are crucial for disease resistance [35]. LA, along with other MCFAs, has been shown to have immunomodulatory properties across various animal species, encouraging its inclusion in diets within the livestock industry [4,36,37].

In the present study, dietary supplementation with lauric acid (LA) demonstrated the potential to modulate the immune system of juvenile European seabass. Notably, the most significant effects were observed at the 1% LA supplementation level, which resulted in a reduction in circulating white blood cells (WBC) and a downregulation of key immune-related genes, including *tnf-α*, *il-10*, *casp3*, and *il-1β* in the anterior intestine. A decrease in WBC count is commonly associated with a reduced expression of immune-related genes, as WBCs play a central role in the regulation of cytokine, chemokine, and antigen receptor expression [38]. Furthermore, neutrophils and macrophages are crucial in the expression of *tnf-α*, *il-1β*, and *il-10*, highlighting the link between WBC dynamics and immune gene expression [39]. In contrast, in Nile tilapia, dietary inclusion of 4 and 6% alpha-monolaurin resulted in a linear increase in WBC count, as well as the expression of *il-1β* and *INF-γ* [6]. Similarly, African catfish fed diets containing 3 and 6% palm oil showed increased hemoglobin (Hb), WBC, and red blood cell (RBC) counts [40], suggesting species-specific immune responses to dietary modifications.

On the other hand, gilthead sea bream (Sparus aurata) fed a diet supplemented with 0.3% coconut fatty acid distillate (DICOSAN®) exhibited a downregulation of *il-8* and no pro-inflammatory response, as evidenced by the absence of changes in intestinal *tnf-α* and *il-1β* expression, as well as in plasma immunological parameters [10]. The authors suggested that this response indicates that neutrophils and macrophages remain inactive until triggered by an external insult, highlighting the potential of MCFAs to maintain immune homeostasis under non-challenged conditions. Overall, the different responses observed emphasize the potential dose-dependent and species-specific immunomodulatory effects of lauric acid and its derivatives on key immune-related gene expression.

5. Conclusions

This study showed that up to 2% dietary LA supplementation promoted growth performance while not affecting feed utilization in European sea bass juveniles. Moreover, 1% LA improved intestinal oxidative and immunological status. Feed intake was directly correlated to the dietary LA level, and further studies are required to understand the mechanisms of action and the potential of using LA as a feed stimulant for this species.

Author Contributions: F.F. was responsible for the experimental trial and for the analytical procedures and wrote the manuscript. N.M. assisted with analytical procedures. R.M. assisted with analytical procedures and manuscript writing. A.O.-T. was responsible for the financial support, designed the experiment, and supervised the manuscript writing. H.P. was responsible for the financial support, designed the experiment, and supervised the manuscript writing. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: The growth trial was conducted at CIIMAR facilities by skilled researchers (following FELASA category C guidelines) in compliance with the European Union Directive (2010/63/EU). All animals were maintained according to the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines, ensuring ethical standards in animal research. The procedures were authorized by the ORBEA Animal Welfare Committee at CIIMAR (reference ORBEA_CIIMAR_27_2019), adhering to the European Union directive 2010/63/EU and the Portuguese legislation DL 113/2013.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data generated during the current study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

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