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Replacement of fish oil with vegetable oil blends in feeds for greater amberjack (*Seriola dumerili*) juveniles: Effect on growth performance, feed efficiency, tissue fatty acid composition and flesh nutritional value

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Abstract

This study was undertaken to assess the effects of fish oil (FO) substitution by a mixture of alternative vegetable oils (VO) on *Seriola dumerili* culture performance. A 154-day feeding experiment was conducted using juveniles (39.2 ± 1.6 g average weight). Three isolipidic and isoenergetic meal-based diets were formulated varying their lipid component. The control diet contained 100% FO (FO100), whereas diets VO50 and VO100 included 1/2 of oil blend and all the oil from blend of palm oil (PO) and linseed oil (LO) as substitute for FO, respectively. Dietary regime did not significantly affect growth performance, biometric indices, feed efficiency, plasma chemistry and liver and muscle lipid contents. Nonetheless, dietary VO inclusion impacted on the fatty acid profile of target tissues, especially in the liver. Fatty acid profiles of the fillets reflected those of the dietary oils except that there was apparent selective utilization of palmitic acid (C16:0) and oleic acid (C18:1n-9) and apparent selective retention of long-chain polyunsaturated fatty acids, especially eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3). The nutritional value and the potential ability to prevent the development of coronary heart diseases of the flesh lipid fraction decreased with gradual FO substitution.

KEYWORDS
alternative oil sources, fatty acid composition, fish oil substitution, greater amberjack, linseed oil, palm oil

1 | INTRODUCTION

Marine fish oils (FO) have conventionally been used as the major dietary lipid component in aquaculture feeds, especially for fast-growing marine carnivorous fish which require the supply of long-chain polyunsaturated fatty acids (LC-PUFA) such as eicosapentaenoic acid (20:5n-3, EPA), docosahexaenoic acid (22:6n-3, DHA) and arachidonic acid (20:4n-6, AA), considered essential fatty acids (EFA) for most marine finfish species. Supplying EFA-balanced diets is indispensable to sustain not only growth, survival and feed efficiency but also health and flesh nutritional quality in cultured specimens (Sargent, Tocher, & Bell, 2002; Tocher, 2010).

Formulating suitable compound feeds is currently one of the main challenges for the aquaculture industry. The fast expansion of aquaculture production worldwide and the increasing demand of marine products along with the declining availability of fish meal (FM) and FO

make relying on finite marine natural resources both economically and environmentally unsustainable (Kaushik, Coves, Dutto, & Blanc, 2004; Tacon & Metian, 2008).

Consequently, replacement of marine ingredients by terrestrial sources in aquafeeds is being a fairly widespread practice looking for suitable alternatives for the long-term sustainability of the aquaculture industry, and vegetable oils (VO) have received an important attention as substitutes of the marine oil due to their comparatively reduced cost, lower concentration of dioxins and other organic pollutants, and their suitable production levels (Sales & Glencross, 2011). Numerous of these studies have covered a wide variety of fish species such as gilthead seabream (Benedito-Palos, Saera-Vila, Calduch-Giner, Kaushik, & Pérez-Sánchez, 2007; Benedito-Palos et al., 2008; Fountoulaki et al., 2009), European seabass (Izquierdo et al., 2003; Mourente & Bell, 2006), red seabream (Huang, Oo, Higgs, Brauner, & Satoh, 2007), turbot (Regost, Arzel, Robin, Rosenlund, & Kaushik, 2003), cobia (Trushenski et al., 2011) and Atlantic salmon (Ruyter, Moya-Falcon, Rosenlund, & Vegusdal, 2006; Torstensen, Li, & Frøyland, 2000). Little or no effect on fish performance has been observed in most of these investigations as far as the minimum EFA requirements were covered. Nonetheless, fish fed VO have shown important modifications in their tissue fatty acid (FA) composition, including increased levels of C18 PUFA and reduced proportions of n-3 LC-PUFA, especially EPA and DHA, which may affect not only fish health (Alves-Martins et al., 2012; Bell & Sargent, 2003; Bell et al., 2001) but also compromise the nutritional quality of flesh for human consumption, as n-3 LC-PUFA are human health-promoting compounds (Khankari et al., 2015; Simopoulos, 2008, 2011, 2016; Siriwardhana, Kalupahana, & Moustaid-Moussa, 2012).

A blend of palm oil (PO) and linseed oil (LO) at a proportion of 4:1 was used in our present work to minimize potential changes derived from dietary substitution of FO. PO has high levels of C16 saturated fatty acids (SFA) and C18 monounsaturated fatty acids (MUFA), which are preferred substrates for energy production in fish species favouring diet-to-tissue transfer of LC-PUFA (Henderson, 1996; Kiessling & Kiessling, 1993), whereas LO is rich in PUFA, especially linolenic acid (C18:3n-3), which may result in tissues and organs of more favourable balanced FA. This combination of VO should supply sufficient energy to maintain high growth, an n-6/n-3 PUFA ratio <1 which is regarded as beneficial to human health and should not be detrimental to fish health (Bell, Tocher, Henderson, Dick, & Crampton, 2003), and moderate levels of linoleic acid (C18:2n-6) trying to avoid an excessive deposition of this fatty acid which is reported as one of the most negative indicators to be taken into account when evaluating alternative lipid sources to FO for aquafeeds (Turchini, Torstensen, & Ng, 2009).

The Carangidae family is a group of fish with exceptional consumer acceptance, considered of great potential for aquaculture diversification (updated by Sicuro & Luzzana, 2016). Recently, several species within this family have been abundantly targeted for research, including the effects of replacing marine ingredients by terrestrial sources in yellowtail kingfish (*Seriola lalandi*) (Bowyer, Qin, Smullen, & Stone, 2012; Bowyer, Rout-Pitt, Bain, Stone, & Schuller, 2012; Bowyer et al., 2013; Collins, Ball, Qin, Bowyer, & Stone, 2014), Japanese yellowtail (*Seriola quinqueradiata*) (Khaoian, Nguyen, Ogita, Fukada, & Masumoto, 2014; Nguyen, Khaoian, Fukada, Suzuki, & Masumoto, 2015; Sarker, Satoh, Kamata, Haga, & Yamamoto, 2012; Seno-O et al., 2008) and pompano (*Trachinotus spp.*) (Lech & Reigh, 2012; Lin et al., 2012; Rossi & Davis, 2012). A further carangid species, the greater amberjack, *Seriola dumerili*, is a carnivorous pelagic fish with a broad geographical distribution, fast growth rate and large size which make it suitable for product diversification and development of value-added products, excellent flesh quality and high market price (Nakada, 2000). However, very scarce knowledge about EFA requirements or FO substitution in this species is available; the studies published till date have focused on the optimization of protein inclusion rates and the search of alternative plant protein sources to FM (Takakuwa, Fukada, Hosokawa, & Masumoto, 2006; Tomás, De La Gándara, García-Gomez, Pérez, & Jover, 2005; Uyan et al., 2009; Vidal, De la Gándara García, Gómez, & Cerdá, 2008).

Therefore, the present study was conducted to determine whether partial 1/2 or total dietary FO substitution by a blend of PO and LO (4:1) affects growth performance, feed efficiency, plasma chemistry and the degree of modification of the FA profile of liver and muscle of greater amberjack (*S. dumerili)* juveniles, including flesh lipid nutritional value. To the best of our knowledge, this work may be considered as the first attempt to assess on the impact of FO replacement in this species.

2 | MATERIALS AND METHODS

2.1 | Fish and rearing conditions

A total of 185 *S. dumerili* juveniles were obtained from a fish farm (Futuna Blue S.A., Cádiz, Spain) and transported to the Fish Nutrition Laboratory of Universitat Politècnica de València (UPV, Spain). Prior to the feeding trial, fish were acclimatized to the experimental rearing conditions for 4 weeks by feeding a standard commercial diet. After this period, groups of 20 fish (average weight 39.2 ± 1.6 g) were randomly distributed into nine 1,750-L cylindrical fibreglass tanks, three tanks per treatment.

The culture was carried out under natural photoperiod conditions in a recirculating seawater system of 75 m^3 capacity equipped with a rotary mechanical filter and a gravity biofilter (6 m^3). During the course of the trial, water temperature (21.5 ± 2.4°C), salinity (31.5 ± 4.1 g/L), pH levels (7.5–8.0) and dissolved oxygen (6.6 ± 1.3 mg/L) were monitored daily.

2.2 | Experimental diets and feeding regime

Three isolipidic and isoenergetic practical feeds were formulated to contain 510 g crude protein and 140 g crude lipid per kilo feed in a dry-weight basis. All ingredients were weighed individually before thoroughly mixed with water to form homogeneous dough and pelleted using a semi-industrial twin-screw extruder (CLEXTRAL BC-45, St. Etienne, France) at the Institute of Animal Science and Technology (UPV). All diets were stored at −20°C for the duration of the trial. Fish

were fed by hand to apparent satiation one of the three experimental diets for 154 days, twice a day (09:00 hr and 17:00 hr), 6 days a week. Any uneaten feed was collected daily to determine fish feed intake (FI).

The ingredients, proximate and FA composition of the experimental diets are shown in Table 1. Briefly, the diet containing FO as the sole lipid source was used as the reference diet (FO100) whereas a blend of VO consisting of PO and LO (4:1) replaced 1/2 and all the oil from oil blend of the FO in the VO50 and VO100 diets, respectively. In all diets,

TABLE 1 Ingredients, proximate and main fatty acid composition of experimental diets

	FO100	VO50	VO100
Ingredients (g/kg)			
Fish meal	525	525	525
Wheat meal	235	235	235
Wheat gluten meal	130	130	130
Fish oil	90	45	0
Linseed oil	0	9	18
Palm oil	0	36	72
Vitamin and mineral premix[a]	20	20	20
Proximate composition			
Dry matter (DM, g/kg wet weight)	886	894	899
Crude protein (g/kg DM)	452	456	461
Crude lipid (g/kg DM)	123	133	135
Ash (g/kg DM)	91	87	87
N free extract (g/kg DM)	237	245	240
Fatty acids (% total fatty acids)			
Total SFA[b]	30.17	33.28	36.13
14:0	5.65	4.24	2.33
16:0	19.96	24.26	28.56
18:0	3.67	3.77	4.17
Total MUFA[b]	22.42	26.09	29.29
16:1[c]	7.74	5.70	3.12
18:1[c]	13.24	18.73	24.94
20:1[c]	0.95	0.79	0.49
22:1[c]	0.50	0.42	0.37
Total PUFA[b]	44.71	38.51	32.87
18:2 n-6	7.04	9.31	11.77
18:3 n-3	1.08	3.14	5.99
18:4 n-3	2.11	1.46	0.83
Total n-6 LC-PUFA	1.13	0.85	0.51
20:4 n-6	0.78	0.56	0.30
22:5 n-6	0.35	0.28	0.21
Total n-3 LC-PUFA[b]	29.19	20.77	12.24
20:5 n-3	15.05	10.70	5.85
22:5 n-3	1.88	1.37	0.84
22:6 n-3	11.06	7.87	5.11
Ratios			
PUFA/SFA	1.48	1.16	0.91
n-6/n-3	0.25	0.40	0.64
DHA/EPA[d]	0.735	0.736	0.874
EPA/ARA[d]	19.178	19.038	19.228

[a]Containing choline, 10 g; DL-α-tocopherol, 5 g; ascorbic acid, 5 g; $Ca_3(PO_4)_2$, 5 g; and a premix, 25 g. This premix contains (per kg) retinol acetate, 1,000,000 IU; calciferol, 500 IU; DL-α-tocopherol, 10 g; menadione sodium bisulphite, 0.8 g; thiamine hydrochloride, 2.3 g; riboflavin, 2.3 g; pyridoxine hydrochloride, 15 g; cyanocobalamine, 25 mg; nicotinamide, 15 g; pantothenic acid, 6 g; folic acid, 650 mg; biotin, 70 mg; ascorbic acid, 75 g; inositol, 15 g; betaine, 100 g; polypeptides 12 g; Zn, 5 g; Se, 20 mg; I, 500 mg; Fe, 200 mg; CuO, 15 g; Mg, 5.75 g; Co, 0.02 g; methionine, 1.2 g; cysteine, 0.8 g; lysine, 1.3 g; arginine, 0.6 g; phenylalanine, 0.4 g; tryptophan, 0.7 g.

[b]Including some minor components not shown.

[c]Including other isomers not shown. Mainly n-7 isomer for C16 and n-9 isomer for C18, C20 and C22.

[d]DHA/EPA, 22:6 n-3/20:5 n-3; EPA/ARA, 20:5 n-3/20:4n-6.

16:0 accounted for the bulk of saturated fatty acids (SFA), 18:1n-9 for monounsaturated fatty acids (MUFA), 18:2n-6 for n-6 PUFA, and EPA and DHA for n-3 LC-PUFA. Moreover, gradual inclusion of the VO mixture increased dietary C16:0 and total SFA (30.2%–36.1% of total FA), C18:1n-9 and total MUFA (22.4%–29.3%), and C18:2n-6 and total n-6 PUFA (8.2%–12.3%) while decreased EPA, DHA and total n-3 PUFA (32.4%–19.1%) despite C18:3n-3 raised from 1.1% to 6.0% of total FA. DHA/EPA and EPA/ARA ratios remained unchanged among diets (Table 1).

2.3 | Fish sampling and growth evaluation

Fish were anaesthetized with 10 mg/L clove oil containing 87% eugenol (Guinama®, Valencia, Spain) for individual weight and fork length measurements at the beginning, end, and regularly at 30-day intervals after the start of the feeding trial. In addition, at the end of the experiment eight fish from each treatment were collected for blood, liver and muscle sampling. Blood was drawn via the ventral aorta using 5-ml heparinized syringes, centrifuged at 3,000 *g* for 5 min at 4°C to separate the plasma which was stored at −30°C until further analyses. Next, the fish were euthanized with an overdose of clove oil and portions of liver and dorsal muscle rapidly excised, frozen in liquid nitrogen and stored at −80°C for subsequent biochemical determinations.

The effect of dietary treatments on culture performance was determined by evaluating growth, survival and nutrient utilization indices, including weight gain (WG), specific growth rate (SGR), feed intake (FI) and feed conversion ratio (FCR) at the end of the feeding trial (Table 2).

All procedures were carried out in accordance with the European Directive 2010/63/EU and Spanish national legislation (Spanish Royal Decree 53/2013), which regulate animal usage in experimentation and/or other scientific purposes.

TABLE 2 Growth performance and feed utilization of *Seriola dumerili* juveniles fed the experimental diets for 154 days

	FO100	VO50	VO100
Initial weight (g)	39.6 ± 3.7	37.9 ± 1.0	40.2 ± 2.9
Final weight (g)	390 ± 23.2	397 ± 24.4	375 ± 30.8
WG (%)[a]	894 ± 96	940 ± 75	840 ± 16
SGR (% per day)[b]	1.49 ± 0.07	1.50 ± 0.05	1.47 ± 0.02
FI (g 100 g fish/day)[c]	1.82 ± 0.26	1.81 ± 0.13	1.79 ± 0.02
FCR[d]	1.75 ± 0.27	1.75 ± 0.14	1.72 ± 0.03
Survival (%)	75 ± 6	74 ± 6	74 ± 7

Data are expressed as mean ± *SD*.
[a]Weight gain = 100 × [(final weight − initial weight)/initial weight]
[b]Specific growth rate = 100 × (ln final weight − ln initial weight)/feeding days
[c]Feed intake = 100 × feed consumption (g)/average biomass (g) x days
[d]Feed conversion ratio = dry food fed (g)/wet weight gain (g).

TABLE 3 Biometric indices and proximate composition of *Seriola dumerili* juveniles fed the experimental diets for 154 days

	FO100	VO50	VO100
CF[1]	1.37 ± 0.17	1.30 ± 0.24	1.28 ± 0.10
VSI (%)[2]	4.32 ± 0.62	4.18 ± 1.10	4.33 ± 0.52
HSI (%)[3]	0.87 ± 0.20	0.78 ± 0.15	0.84 ± 0.10
MSI (%)[4]	0.18 ± 0.17	0.05 ± 0.15	0.10 ± 0.09
IFR (%)[5]	38.4 ± 4.17	34.1 ± 3.23	34.6 ± 4.60
IER (%)[6]	21.7 ± 0.91	20.6 ± 1.12	21.4 ± 0.83
Whole-body proximate composition g/kg w.w.			
Moisture	696.5 ± 0.9[a]	706.3 ± 0.9[b]	702.5 ± 0.2[ab]
Crude protein	192.2 ± 1.3	189.1 ± 1.5	188.7 ± 2.3
Total lipid	77.8 ± 2.9	72.9 ± 2.0	74.7 ± 1.6
Ash	28.1 ± 0.9	27.6 ± 0.3	26.9 ± 0.8

w.w., wet weight; data are expressed as mean ± *SD*. Means with different superscript letters are significantly different ($p < .05$).
[1]Condition factor = 100 × (final weight/total length[3])
[2]Viscerosomatic index = 100 × (viscera weight/final weight)
[3]Hepatosomatic index = 100 × (liver weight/final weight)
[4]Mesenteric fat index = 100 × (viscera fat/final weight)
[5]Ingested fat retention = 100 × (fish fat gain/crude fat intake)
[6]Ingested energy retention = 100 × (fish energy gain, kJ/gross energy intake, kJ).

2.4 | Analytical procedures

Plasma glucose concentration (mg/dl) and activities of glutamate–oxalacetate transaminase (GOT) (AST) (EC 2.6.1.1) and glutamate–pyruvate transaminase (GPT) (ALT) (EC 2.6.1.2) (U/L 37°C) were determined by enzymatic kits according to the manufacturer's instructions (Human, Wiesbaden, Germany). One unit (U) of aminotransferases activity was defined as 1 μmol of NADH disappearance per minute. Concentrations of triglyceride (mg/dl) and cortisol (ng/ml) were measured with a diagnostic kit (Gernon, Barcelona, España) and an enzyme immunoassay kit (Arbor Assays, MI, USA), respectively. Lipase (E.C. 3.1.1) activity (U/L 30°C) was assayed by slight modifications of the method previously described by Gisbert, Giménez, Fernández, Kotzamanis, and Estevez (2009) considering one unit of activity equivalent to 1 μmol of p-nitrophenol myristate hydrolysed per min.

Proximate composition of the experimental diets and whole-body fish were determined according to the following procedures: moisture by oven thermal drying at 110°C to constant weight, ash by combustion in a muffle at 550°C overnight, and crude protein (N x 6.25) by sample digestion using the Kjeldahl method. Quantification of crude fat was performed by ether extraction with an Ankom XT10 Extraction System (NY, USA) (AOCS, 2005). Energy was calculated according to Brouwer (1965), from the C (g) and N (g) balance (GE = 51.8 × C − 19.4 × N).

Liver and muscle total lipid (TL) was extracted by homogenization in chloroform/methanol (2:1, v/v) according to Folch, Lees, and Sloane-Stanley (1957). The organic solvent was evaporated under a stream of nitrogen, the lipid content gravimetrically determined (Christie, 1982) and stored in chloroform/methanol (2:1) containing 0.01% butylated hydroxytoluene (BHT) at −20°C until further analysis. The lipid extract was subjected to acid-catalysed transmethylation with 1% sulphuric acid (v/v) in methanol, and the resultant fatty acid methyl esters (FAME) purified by thin layer chromatography (TLC) (Christie, 1982). During acid-catalysed transmethylation, FAME are formed simultaneously with dimethyl acetals (DMA) which originate from the 1-alkenyl chain of plasmalogens. FAME and DMA were separated and quantified on a TRACE-GC Ultra gas chromatograph (Thermo Scientific, Milan, Italy) equipped with an on-column injector, a flame ionization detector and a fused silica capillary column, Supelcowax TM 10 (30 m × 0.32 mm × 0.25 μm film thickness) (Supelco Analytical, Bellefonte, PA, USA). Helium at a flow of 1.5 ml/min was used as the carrier gas. Individual FAME and DMA were identified by reference to authentic standards, and further confirmation of identity was carried out by mass spectrometry when necessary.

2.5 | Indices of the nutritional quality of lipids

The influence of increasing levels of FO substitution on the nutritional quality of the fish fillet lipid fraction was monitored through indices based on the functional effects of its constituent FA. Equations (1–3) were used to determine the index of atherogenicity (IA) (Ulbricht & Southgate, 1991), the index of thrombogenicity (IT) (Ulbricht & Southgate, 1991), and the flesh lipid quality (FLQ) (Abrami et al., 1992), respectively.

$$IA = \frac{C12{:}0 + (4 * C14{:}0) + C16{:}0}{\sum \text{MUFA} + \text{n6 PUFA} + \text{n3 PUFA}} \quad (1)$$

$$IT = \frac{C14{:}0 + C16{:}0 + C18{:}0}{(0.5 * \sum \text{MUFA} + 0.5 * \text{n6 PUFA} + 3 * \text{n3 PUFA}) + (\text{n3 PUFA}/\text{n6 PUFA})} \quad (2)$$

$$FLQ = \frac{C20{:}5n-3 + C22{:}6n-3}{\sum \text{total FA}} \quad (3)$$

Briefly, the two-first indices indicate that C12:0, C14:0 and C16:0 are atherogenic (favouring the adhesion of lipids to cells of the immunological and circulatory systems), and that C14:0, C16:0 and C18:0 are thrombogenic, facilitating the formation of clots in the blood vessels. The third equation, reveals the percentage relationship in which the main n-3 LC-PUFA (EPA and DHA) appear in muscle with respect to the totality of the lipids.

2.6 | Statistical analysis

Prior to analysis, all data expressed as percentage were arcsine-transformed. Normal distribution was checked with the Kolmogorov–Smirnov test and homogeneity of variances by the Levene test. Comparisons among dietary groups (FO100, VO50 and VO100) were assessed by one-way ANOVA and significant differences identified by the Tukey post hoc test. When homoscedasticity and/or normality was not achieved, data were subjected to the nonparametric Kruskal–Wallis test followed by the Games–Howell test for post hoc comparisons. Differences among means were accepted when $p < .05$. Statistical analyses were carried out using the SPSS package version 20.0 for Windows (SPSS, Inc., Chicago, IL, USA).

3 | RESULTS

3.1 | Growth performance and feed utilization

At the end of the feeding period, no negative effects were found with either the partial half of the fish oil or complete FO substitution with the mixture of PO and LO (4:1) in growth and feed performance, although values were generally numerically inferior in fish fed the no-FO diet. Briefly, all dietary groups presented similar final body weight (390, 397 and 375 g for FO100, VO50 and VO100, respectively) which resulted in steady weight gains of 894%, 940% and 840%, respectively. All diets were readily accepted by the fish, with the mean daily FI being 1.81 g 100 g fish/day, and the average FCR, 1.74. Final survival rate was 75% for all dietary groups (Table 2).

3.2 | Biometric parameters and body proximate composition

None of the somatic parameters studied (condition factor, viscerosomatic, hepatosomatic and mesenteric fat indices, ingested fat retention and ingested energy retention) significantly varied with increasing FO replacement (Table 3). Similarly, no trend in protein, lipid or ash of fish whole body was apparent in dietary groups. Only moisture content varied among treatments, being significantly lower in fish fed the control diet (FO100) than in those receiving VO50.

3.3 | Plasma biochemical determinations

As it is shown in Table 4, glucose, triglyceride and cortisol concentrations remained fairly constant among treatments (186–223 mg/dl, 89–98 mg/dl, and 54–56 ng/ml, respectively). Likewise, the activities of the enzymes GOT (10.9–20.6 U/L), GPT (3.9–6.1 U/L) and lipase (7.1–7.8 U/L) were not affected by the diet.

3.4 | Tissue biochemical composition

The TL contents of liver and muscle did not vary among treatments, neither when compared to the initial sample, although the liver presented significantly higher values than muscle ranging from 79 to 88 g/kg of fresh weight, and 7.3 to 9.5 g/kg of fresh weight, respectively (Figure 1). Both tissues followed similar patterns of FA profiles and variations with respect to the initial sample in response to increasing FO substitution (Tables 5 and 6, respectively). Briefly, despite the relative proportion of C16:0 was higher in fish fed the no-FO diet (VO100), no significant variations among treatments existed in the total percentage of SFA. Total MUFA raised significantly with higher VO inclusion, whereas total PUFA, n-6 and n-3 LC-PUFA showed the opposite trend. Individually, C18:1n-9 (which represented 50%–80% of total MUFA), C18:2n-6 and C18:3n-3 were higher when complete FO substitution, whereas ARA, EPA, C22:5n-3 (DPA, docosapentaenoic acid) and DHA, reached higher values in fish fed the VO100 diet. Hepatic DHA/EPA ratio increased and EPA/ARA ratio decreased with reduced dietary FO (Table 5), which, conversely, remained unchanged in muscle (Table 6).

Muscle and liver showed a tissue-specific fatty acid profile, with muscle containing lower proportions of MUFA, and higher PUFA, n-3 and n-6 LC-PUFA than liver. DMA were present exclusively in muscle (2.5%–3.0% of total FA). Irrespective to diet, C18 MUFA and C18:2n-6 proportions were 1.5 to 2-fold lower in muscle than in the liver (9.2, 12.7 and 16.5 versus 15.9, 23.9 and 29.7;, 7.2 and 10.7 versus 9.7, 12.4 and 15.3, respectively), whereas C22:6n-3 was 3 to 4-fold higher

TABLE 4 Plasma parameters of greater amberjack juveniles fed the experimental diets for 154 days

	FO100	VO50	VO100
Glucose (mg/dl)	223.4 ± 31.8	190.9 ± 24.3	185.9 ± 32.4
GOT (U/L)	20.6 ± 8.8	12.6 ± 2.8	10.9 ± 1.2
GPT (U/L)	6.1 ± 1.4	4.9 ± 1.1	3.9 ± 0.8
Triglycerides (mg/dl)	94.4 ± 12.3	89.0 ± 21.4	97.8 ± 12.7
Cortisol (ng/ml)	54.2 ± 16.0	56.1 ± 11.5	55.2 ± 8.7
Lipase (U/L)	7.8 ± 0.9	7.6 ± 0.5	7.1 ± 0.5

Data are expressed as mean ± *SD* ($n = 3$).

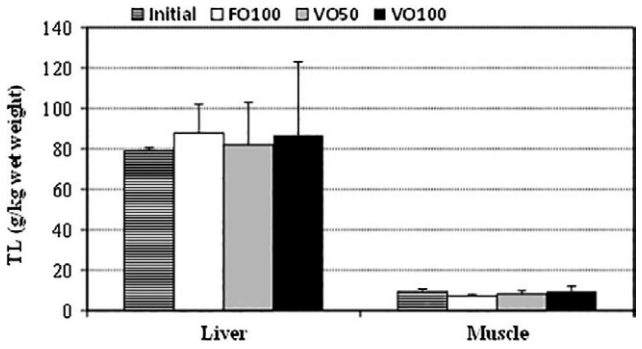

FIGURE 1 Total lipid content (g/kg wet weight) of liver and muscle of *S. dumerili* juveniles fed the experimental diets for 154 days. The bars represent the mean of N replicates plus the *SD*

in the muscle (29.7, 26.9 and 22.2 versus 9.9, 7.2 and 5.4% of total FA, respectively).

3.5 | Indices of the nutritional quality of lipids

The indices used to assess the nutritional value of the flesh lipid fraction are shown in Table 6. Both PUFA/SFA and n-6/n-3 ratios were more favourable in terms of nutritional value in fish fed the diet with FO as the unique lipid source, decreasing with higher inclusion of the VO mixture. IA remained unchanged irrespective of dietary FO substitution (0.38-0.40) whereas complete FO replacement promoted a significant increase in IT (0.25 ± 0.01) compared to FO100 and VO50-fed fish (0.21 ± 0.01 and 0.22 ± 0.01, respectively). Finally, FLQ decreased with gradual FO replacement (39.39 ± 1.83, 34.88 ± 3.09 and 28.63 ± 2.89, respectively).

4 | DISCUSSION

In the present study, the plant-based oil mixture consisting of PO and LO (4:1) used to partially (50%) or totally substitute FO did not significantly affect greater amberjack, *S. dumerili* growth performance and feed efficiency (Table 2). Both SGR and FCR of fish fed the VO-based blend are similar or even better than most values reported for fish of the same size class fed either fish scraps or FO-based diets in the western Mediterranean coast (reviewed by Mazzola, Favaloro, & Sará, 2000).

A number of previous studies have reported that a large fraction aproximately 2/3 of dietary FO may be replaced by VO blends without compromising fish production (Benedito-Palos et al., 2008; Fountoulaki et al., 2009; Izquierdo et al., 2003; Menoyo et al., 2004; Mourente & Bell, 2006; Peng et al., 2008). However, some species are negatively affected by total substitution of FO (Nasopoulou & Zabetakis, 2012; Regost et al., 2003; Sales & Glencross, 2011) while other reports show not effect (Glencross et al., 2016; Mozanzadeh et al., 2016), so it becomes necessary to study carefully FO substitution effects for any particular fish species. Big pelagic marine carnivorous fish species such as *S. quinqueradiata* did not vary growth performance when receiving diets with increasing olive oil inclusion to completely replace FO (Seno-O et al., 2008) in a short-term feeding trial of 40 days. On the contrary, both cobia (*Rachycentron canadum*) and yellowtail kingfish (*S. lalandi*) juveniles production performance was compromised when FO was totally substituted by sunflower or canola oil, respectively (Bowyer, Qin et al., 2012; Trushenski et al., 2011). Overall, successful fish performance may be achieved when FO sparing with alternative oils of terrestrial origin as long as their minimum EFA requirements are met. In our work, FO100, VO50 and VO100 diets provide 2.7, 2.1 and 1.2% n-3 LC-PUFA of dry matter respectively, which is sufficient to cover the EFA requirements for most marine fish species (Glencross, 2009; Tocher, 2010). Consequently, although *S. dumerili* nutritional requirements are still unknown and the EFA requirements vary qualitatively and quantitatively with both species and growth stage, it seems that formulation with 525 g/kg of FM contributes to supply enough LC-PUFA to meet fish needs even in the absence of FO, as FM usually contains up to 80-150 g of crude lipid/kg feed, with a 300-350 g/kg of n-3 LC-PUFA (Bimbo, 2000). In fact, our present results seem to indicate that the EFA requirements of greater amberjack juveniles may be met by levels of n-3 LC-PUFA up to 12 g/kg of the dry weight of the diet. As far as we know, this is the first reference on the quantitative EFA requirements for this species.

Regardless of whether FO replacement affects fish growth and feed performance, its impact on tissue lipid deposition and fatty acid composition is controversial, varying depending on the species, dietary lipid content and substitute lipid source (Turchini et al., 2009). Previous research suggest that SFA- and MUFA-rich lipid diets can make LC-PUFA utilization and/or diet-to-tissue transfer more efficient (Bowzer, Jackson, & Trushenski, 2016; Pérez, Rodríguez, Bolaños, Cejas, & Lorenzo, 2014; Turchini et al., 2009). The PO:LO (4:1) mixture used here seem to provide balanced proportions of SFA: MUFA: PUFA and n-6/n-3 ratio for maintaining or even improving DHA/EPA and EPA/ARA ratios in muscle (3.3 and 5.6 for VO50; 3.4 and 5.7, for VO100, respectively) with respect to the initial fish (2.32 and 7.48) and fish receiving the total replaced FO diet (3.0 and 5.8, respectively). The same tendency for both proportions was observed in the liver of VO-fed groups (0.76 and 9.10; 0.74 and 10.53; 0.88 and 8.79; 1.17 and 7.53; for the initial, FO100, VO50 and VO100 fish, respectively). In addition, physiologically important DHA/EPA and EPA/ARA ratios obtained in our present work are similar to those previously reported for farmed greater amberjack adults and similar to wild counterparts (Rodríguez-Barreto et al., 2012; Saito, 2012).

The liver is the major site of lipid storage in the majority of marine fish species being commonly used as indicator of unsuitable dietary fat ingestion. The diagnosis of healthy liver should allow optimized diets to be devised for a given species. It is well established that replacing dietary FO by terrestrial oils may produce the accumulation of fat in fish liver giving rise to a fatty liver syndrome (Benedito-Palos et al., 2008; Díaz-López et al., 2010; Piedecausa, Mazón, García-García, & Hernández, 2007; Sargent et al., 2002), which may be associated with increased lipid peroxidation and impaired function such as inefficient nutrient utilization and necrosis (Craig, Washburn, & Gatlin, 1999; Tucker, Lellis, Vermeer, Roberts, & Woodward, 1997). In our study, both

TABLE 5 Total FA (g kg/DM) and main fatty acid composition (% total fatty acids) of liver TL from cultured *Seriola dumerili* juveniles fed the experimental diets for 154 days

	Initial	FO100	VO50	VO0
Total FA	211.74 ± 29.09	191.63 ± 20.2	222.07 ± 16.3	186.53 ± 24.6
Total SFA[1]	30.31 ± 1.00	30.25 ± 0.89	31.54 ± 0.86	31.28 ± 2.50
14: 0	4.96 ± 0.18	4.62 ± 0.23^{c}	2.95 ± 0.12^{b}	1.69 ± 0.10^{a}
16: 0	20.52 ± 0.87	20.33 ± 0.76^{a}	22.71 ± 1.03^{b}	23.85 ± 2.30^{b}
18: 0	3.63 ± 0.16	4.24 ± 0.45	5.04 ± 0.47	4.99 ± 0.61
Total MUFA[1]	28.39 ± 1.62	24.92 ± 1.03^{a}	30.52 ± 1.32^{b}	33.86 ± 1.68^{b}
16: 1[2]	9.27 ± 0.18	7.71 ± 0.06^{c}	5.39 ± 0.05^{b}	3.22 ± 0.09^{a}
18: 1[2]	18.08 ± 1.14	15.89 ± 1.22^{a}	23.92 ± 0.92^{b}	29.73 ± 1.56^{c}
20: 1[2]	0.61 ± 0.18	0.55 ± 0.06	0.52 ± 0.08	0.54 ± 0.16
Total PUFA[1]	38.16 ± 2.65	43.92 ± 0.90^{b}	37.37 ± 1.13^{a}	34.48 ± 1.81^{a}
18: 2 n-6	8.80 ± 0.36	9.70 ± 0.31^{a}	12.40 ± 0.72^{b}	15.31 ± 1.09^{c}
18: 3 n-3	0.93 ± 0.04	1.23 ± 0.11^{a}	3.25 ± 0.03^{b}	5.29 ± 0.66^{c}
18: 4 n-3	1.29 ± 0.16	1.32 ± 0.14^{c}	0.73 ± 0.03^{b}	0.29 ± 0.05^{a}
Total n-6 LC-PUFA[1]	1.56 ± 0.06	1.96 ± 0.16^{c}	1.47 ± 0.06^{b}	1.13 ± 0.09^{a}
20: 2 n-6	nd	0.26 ± 0.05	0.29 ± 0.05	0.31 ± 0.09
20: 4 n-6	1.26 ± 0.05	1.28 ± 0.08^{c}	0.92 ± 0.03^{b}	0.61 ± 0.09^{a}
22: 5 n-6	0.29 ± 0.02	0.29 ± 0.01^{b}	0.20 ± 0.03^{a}	0.18 ± 0.04^{a}
Total n-3 LC-PUFA[1]	23.77 ± 2.65	27.75 ± 0.87^{c}	18.50 ± 0.71^{b}	12.03 ± 1.04^{a}
20: 4 n-3	0.76 ± 0.01	0.94 ± 0.12^{c}	0.67 ± 0.06^{b}	0.34 ± 0.05^{a}
20: 5 n-3	11.50 ± 1.03	13.48 ± 0.31^{c}	8.07 ± 0.31^{b}	4.59 ± 0.30^{a}
21: 5 n-3	0.39 ± 0.03	0.46 ± 0.01^{c}	0.31 ± 0.01^{b}	0.16 ± 0.01^{a}
22: 5 n-3	2.37 ± 0.13	2.92 ± 0.35^{c}	2.28 ± 0.22^{b}	1.43 ± 0.06^{a}
22: 6 n-3	8.75 ± 1.46	9.95 ± 1.12^{b}	7.18 ± 0.89^{a}	5.36 ± 1.19^{a}
Ratios				
PUFA/SFA	1.26 ± 0.13	1.45 ± 0.04^{b}	1.19 ± 0.03^{a}	1.11 ± 0.13^{a}
n-6/n-3	0.40 ± 0.05	0.39 ± 0.02^{a}	0.62 ± 0.06^{b}	0.93 ± 0.06^{c}
DHA/EPA[3]	0.76 ± 0.06	0.74 ± 0.07^{a}	0.88 ± 0.04^{a,b}	1.17 ± 0.23^{b}
EPA/ARA[3]	9.10 ± 0.53	10.53 ± 0.66^{b}	8.79 ± 0.42^{a,b}	7.53 ± 1.23^{a}

Results are expressed as means ± *SD* (n = 3). Means with different superscript letters indicate significant differences (p < .05), nd = not detected.
[1]Including some minor components not shown.
[2]Including other isomers not shown. Mainly n-7 isomer for C16 and n-9 isomer for C18 and C20.
[3]DHA/EPA, 22:6 n-3/ 20:5 n-3; EPA/ARA, 20:5 n-3/ 20:4 n-6.

the liver fat content and the HSI of VO50- and VO100-fed fish were similar to the control and initial fish, suggesting no hepatic affection with increasing levels of PO:LO inclusion. These observations agree well with previous research on turbot (*Psetta maxima*) (Regost et al., 2003), European seabass (Richard, Mourente, Kaushik, & Corraze, 2006) and gilthead seabream (Bouraoui et al., 2011) where no impairment of lipogenic activity and lipid content in fish liver was detected when using PO and/or LO to replace FO. In line with this, Lemaire et al. (1991) found correlations between plasma biochemical parameters and hepatic histopathological condition. Thus, plasma parameters are often regarded as suitable monitoring tools of the physiological status of the fish (Bowyer, Qin et al., 2012; Coz-Rakovac et al., 2008; Díaz-López et al., 2009; Kowalska et al., 2012) and could also be used as physiological indicators of lipogenesis affection with FO substitution (Richard et al., 2006). Under our experimental conditions, the inclusion of PO and LO did not affect plasma chemistry suggesting that fish were in acceptable nutritional status adding more evidences to the proper hepatic functioning even under FO absence. However, the higher relative content of C18:1n-9 and C18:2n-6, along with lower proportions of LC-PUFA, especially ARA, EPA and DHA, in the liver of VO-fed fish might have a long-term detrimental impact on lipid/lipoprotein metabolism, as they have been reported to modulate lipid metabolism at different levels (reviewed by Turchini et al., 2009). Thus, longer-term studies are needed to rule out possible hepatic damage caused by the PO:LO mixture not detected in the present 5-month feeding trial.

Regardless of dietary inputs, muscle displayed higher relative content of n-3 LC-PUFA than the liver or diet. This indicates that LC-PUFA, particularly DHA, are selectively retained in greater amberjack fillets, as previously reported in salmon (Bell, McGhee, Campbell, &

TABLE 6 Total FA (g kg/DM) and main fatty acid composition (% total fatty acids) of muscle TL, and indices of nutritional quality of lipids from cultured *Seriola dumerili* juveniles fed the experimental diets for 154 days

	Initial	FO100	VO50	VO100
Total FA	33.04 ± 6.45	16.95 ± 2.47	20.31 ± 4.93	23.94 ± 6.34
Total SFA[1]	28.44 ± 1.70	34.28 ± 0.28	33.64 ± 0.76	33.36 ± 0.47
14: 0	2.47 ± 0.38	1.09 ± 0.29	0.95 ± 0.26	0.69 ± 0.13
16: 0	17.79 ± 1.06	20.51 ± 0.17^{a}	20.44 ± 0.05^{a}	21.07 ± 0.12^{b}
18: 0	7.27 ± 0.61	9.36 ± 0.22	9.38 ± 0.71	8.76 ± 0.37
Total MUFA[1]	20.22 ± 0.14	12.92 ± 1.41^{a}	16.15 ± 2.20^{a,b}	19.24 ± 2.32^{b}
16: 1[2]	5.27 ± 0.50	2.67 ± 0.48^{b}	2.22 ± 0.44^{a,b}	1.73 ± 0.27^{a}
18: 1[2]	13.31 ± 0.44	9.19 ± 0.87^{a}	12.71 ± 1.79^{a,b}	16.46 ± 2.15^{b}
20: 1[2]	0.76 ± 0.14	0.33 ± 0.06	0.32 ± 0.04	0.31 ± 0.04
Total PUFA[1]	49.20 ± 2.13	51.71 ± 1.42^{b}	49.83 ± 1.61^{a,b}	47.13 ± 1.90^{a}
18: 2 n-6	5.08 ± 0.11	4.70 ± 0.30^{a}	7.14 ± 0.52^{b}	10.69 ± 0.32^{c}
18: 3 n-3	0.65 ± 0.04	0.38 ± 0.01^{a}	1.38 ± 0.29^{b}	2.59 ± 0.31^{c}
18: 4 n-3	0.91 ± 0.16	0.39 ± 0.08^{b}	0.30 ± 0.07^{b}	0.18 ± 0.04^{a}
Total n-6 LC-PUFA[1]	2.01 ± 0.06	2.60 ± 0.12^{b}	2.37 ± 0.25^{a,b}	2.02 ± 0.25^{a}
20: 2 n-6	nd	0.14 ± 0.01^{a}	0.18 ± 0.01^{b}	0.19 ± 0.01^{b}
20: 4 n-6	1.43 ± 0.05	1.65 ± 0.08^{b}	1.44 ± 0.15^{a,b}	1.18 ± 0.17^{a}
22: 5 n-6	0.58 ± 0.03	0.72 ± 0.06	0.72 ± 0.08	0.64 ± 0.07
Total n-3 LC-PUFA[1]	39.29 ± 2.06	43.08 ± 1.80^{c}	38.26 ± 2.34^{b}	31.45 ± 2.34^{a}
20: 4 n-3	0.52 ± 0.11	0.29 ± 0.03^{b}	0.30 ± 0.04^{b}	0.20 ± 0.02^{a}
20: 5 n-3	10.73 ± 1.29	9.78 ± 0.43^{c}	8.02 ± 0.24^{b}	6.40 ± 0.50^{a}
21: 5 n-3	0.35 ± 0.04	0.19 ± 0.03^{b}	0.20 ± 0.04^{b}	0.14 ± 0.02^{a}
22: 5 n-3	3.05 ± 0.22	2.87 ± 0.07^{b}	2.87 ± 0.08^{b}	2.47 ± 0.07^{a}
22: 6 n-3	24.64 ± 1.55	29.65 ± 2.33^{b}	26.86 ± 2.88^{a,b}	22.23 ± 2.06^{a}
Total DMA[1]	1.02 ± 0.11	2.91 ± 0.04	2.77 ± 0.35	2.57 ± 0.46
16: 0 DMA	0.63 ± 0.03	1.50 ± 0.08	1.48 ± 0.17	1.45 ± 0.31
18: 0 DMA	0.39 ± 0.11	0.79 ± 0.05^{b}	0.72 ± 0.07^{a,b}	0.63 ± 0.06^{a}
Ratios				
PUFA/SFA	1.74 ± 0.17	1.51 ± 0.04^{b}	1.48 ± 0.03^{a,b}	1.41 ± 0.04^{a}
n-6/n-3	0.17 ± 0.01	0.17 ± 0.01^{a}	0.24 ± 0.02^{b}	0.37 ± 0.02^{c}
DHA/EPA[3]	2.32 ± 0.33	3.02 ± 0.34	3.34 ± 0.19	3.46 ± 0.12
EPA/ARA[3]	7.48 ± 0.70	5.93 ± 0.19	5.56 ± 0.51	5.42 ± 0.39
IA		0.40 ± 0.02	0.39 ± 0.03	0.38 ± 0.02
IT		0.21 ± 0.01^{a}	0.22 ± 0.01^{a}	0.25 ± 0.01^{b}
FLQ		39.39 ± 1.83^{b}	34.88 ± 3.09^{b}	28.63 ± 2.89^{a}

Results are expressed as means ± *SD* (n = 3). Means with different superscript letters indicate significant differences (p < .05), nd = not detected.
[1]Including some minor components not shown.
[2]Including other isomers not shown. Mainly n-7 isomer for C16 and n-9 isomer for C18 and C20.
[3]DHA/EPA, 22:6 n-3/ 20:5 n-3; EPA/ARA, 20:5 n-3/ 20:4 n-6.

Sargent, 2003; Bell et al., 2001; Torstensen, Frøyland, & Lie, 2004), and other marine fish species (Bowyer, Qin et al., 2012; Mourente & Bell, 2006; Pérez et al., 2014). The high supply of SFA, especially C14:0 and C16:0, and MUFA, chiefly C18:1n-9, in VO50 and VO100 diets may have promoted their preferential use as metabolic energy for swimming (Bell, McGhee et al., 2003; McKenzie, 2001; Stubhaug, Lie, & Torstensen, 2007; Torstensen et al., 2004) enhancing muscle deposition of LC-PUFA.

There is currently increasing interest on the intake of marine-based feedstuff for its health-promoting benefits to humans. Several FA ratios and indices have been defined to assess the nutritional quality of food lipid for human consumption. According to nutritional recommendations, the PUFA/SFA ratio in human diets should be above 0.45 (Wood et al., 2004) and, within the PUFA, a ratio of 1:1 to 2:1 n-6/n-3 should be the target ratio for health (Simopoulos, 2011). Lower ratios of PUFA/SFA in the diet may increase the incidence of cardiovascular

disease (WHO 2003). Further, fats with lower indices of atherogenicity (IA) and thrombogenicity (IT) can inhibit the aggregation of platelets and decrease the levels of esterified FA, cholesterol and phospholipids, thereby preventing the appearance of micro- and macrocoronary diseases (Turan, Sönmez, & Kaya, 2007). The indices of lipid quality selected in the present work clearly indicate that flesh from greater amberjack juveniles is a nutritionally adequate food for human consumption although the gradual inclusion of the PO:LO mixture tended to partially reduce its value. In brief, and regardless of dietary treatment, both PUFA/SFA and n-6/n-3 are well within values recommended for healthy human. Although there is no recommended values for IA and IT, it is generally accepted that the lower the values the healthier the ratios. So, the low values of both IA and IT indices together with high FLQ present in flesh suggest that its consumption may help to prevent the development of coronary heart diseases, being more favourable in terms of lipid quality for human consumption than gilthead seabream or European seabass (Grigorakis, 2007; Pérez et al., 2014).

In summary, the present work provides valuable information to the successful and economically viable culture of greater amberjack. The mixture of PO and LO (4:1) can effectively replace completely dietary FO in FM-based diets for *S. dumerili* juveniles without affecting growth performance, feed utilization and fish health. Based on these results, it appeared that a 12 g/kg of EFA in a dry-weight basis may cover the EFA requirements for juveniles of this species. In terms of product quality, and regardless of dietary lipid, flesh of cultured specimens displayed good nutritional and healthy characteristics for human consumption, in line with current global guidelines for fat intake.

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