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The effect of dietary taurine and its potential biosynthesis on juvenile grey mullet (*Mugil cephalus*) performance

William Koven*, Chen Bracha, Oriya Nixon, Dor Israeli, Amos Tandler, Iris Meiri-Ashkenazi, Hanna Rosenfeld

Israel Oceanographic and Limnological Research, the National Center for Mariculture, Eilat 88112, Israel

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Abstract

The grey mullet is a catadromous species that spawns in the taurine-rich seawater environment, followed by the young fish generally migrating to less saline, low taurine waters during the larva-juvenile transition. Consequently, this study aimed to (1) determines whether there is a dietary taurine requirement in juvenile grey mullet for enhanced growth and (2) the potential for taurine biosynthesis. The experimental system consisted of sixteen 400-l V-tanks, where filtered, UV-treated ambient seawater (40 ‰) entered the bottom of the tanks at a rate of 7 tank exchanges/day. This allowed the testing of four 1 mm pelleted diets (0, 0.5, 1.0, and 2.0% taurine DW diet) in replicates of 4 tanks/treatment for 58 days. Grey mullet juveniles demonstrated ($P<0.05$) a specific requirement for a 0.5% taurine DW diet for improved growth. Fish fed the taurine diets displayed populations with a markedly ($P < 0.05$) higher average number of surviving fish (23.4±1.1) of moderately sized (10-20 g) cohorts than smaller (< 10 g) individuals (12.5±1.1). In contrast, the fish fed the taurine control (0% taurine) exhibited similar average numbers of small and moderate sized fish (18.0±3.6-20.0±4.1). Dietary taurine accumulated highly ($P<0.05$) in the muscles in a dose dependent manner but less so ($P<0.05$) in eyes, and liver. The gene expression of liver cysteine sulfinic acid decarboxylase (CSD) exhibited an upregulation ($P<0.05$) with taurine diets from 0 to 1% but was down regulated ($P<0.05$) in fish fed the 2% taurine DW diet.

* Corresponding author. bmkoven@gmail.com

Introduction

The β-amino sulfinic acid taurine promotes fish growth through its roles in bile salt synthesis, anti-oxidative defense, and cellular osmoregulation, as well as its influence on visual, neural, and muscular function (Gaon et al. 2020; Gaon et al. 2021). Taurine has been shown to enhance the gene expression of cholesterol 7 α-hydroxylase (Cyp7α1), a rate-limiting enzyme of bile acid biosynthesis (Lam et al. 2006), as well as its activity in animals (Bellentani et al. 1987; Yokogoshi and Oda 2002) and fish (Tong et al. 2019). As a major contributor to bile salt synthesis, taurine facilitates lipid emulsification and digestion by increasing the activity of bile salt-activated lipase (Gjellisvik et al. 1992), which leads to improved tissue incorporation of fatty acids (Kim et al. 2007). Additionally, taurine enhances the conversion of cholesterol to bile salts by suppressing the acyl CoA cholesterol acyltransferase (ACAT) activity, which binds free cholesterol to a fatty acid (Fakuda et al. 2011). This results in additional cholesterol available for bile salt synthesis and decreases the hepatic metabolic pool of cholesterol (Fukuda et al. 2011). In white grouper (*Epinephelus aeneus*), a dietary taurine correlation with its accumulation in various tissues was ranked as muscles > liver > eyes (Koven et al. 2016). These authors suggested that dietary taurine supplementation enhanced bile salt production resulting in markedly increased levels of total lipid and fatty acid classes, particularly the polyunsaturated fatty acids in the eyes (Koven et al. 2016).

As the marine environment is substantially rich in taurine (Clifford et al. 2017), energetically, it makes sense to satisfy the requirement of this important nutrient through food and not by biosynthesis. Consequently, a dietary taurine requirement has been shown for marine teleosts such as juvenile yellowtail (*Seriola quinqueradiata*; Takagi et al. 2008), bluefin tuna (*Thunnus thynnus*; Yokoyama et al. 2001), skipjack (*Katsuwonus pelamis*; Yokoyama et al. 2001), Japanese flounder (*Paralichthys olivaceus*; Kim et al. 2005) and red sea bream (*Pagrus major*; Matsunari et al. 2008a, b). This was likely due to a deficiency in cysteine sulfinic acid decarboxylase (CSD), a rate-limiting enzyme catalyzing the decarboxylation of cysteine sulfinate to hypotaurine in the main taurine biosynthesis pathway (Park et al. 2002). The requirement for dietary taurine was further reinforced in studies testing the efficacy of replacing fish meals with taurine-poor, plant-based proteins in marine species (Koven et al. 2016) such as juvenile white seabass (*Atractoscion nobilis*; Jirsa et al. 2014), golden pompano (*Trachinotus ovatus*; Wu et al. 2015), totoaba (*Totoaba macdonaldi*; López et al. 2015) and white grouper (*Epinephelus aeneus*; Koven et al. 2016).

Freshwater omnivorous/herbivorous species exhibit varying levels of taurine biosynthesis capability, as the freshwater environment tends to be taurine-poor (Koven et al. 2018). The common freshwater carp (*Cyprinus carpio*) does not appear to have a dietary taurine requirement (Kim et al. 2008) as it accumulates taurine in its tissues while expressing low CSD activity (Yokoyama et al. 2001). This suggests an alternate synthesis route, such as the cysteamine pathway, where cysteine is converted into cysteamine and then into hypotaurine by cysteamine dioxygenase (ADO) (Haga et al. 2017). However, this is considered a secondary pathway in mammals (Stipanuk 2004).

In contrast, studies on the freshwater rainbow trout (Yokoyama and Nakazoe 1992), channel catfish (*Ictalurus punctatus*; Robinson et al. 1978) and Atlantic salmon (*Salmo salar*; Espe, et al. 2012) reported that these species displayed taurine synthesis capability through the CSD pathway. Nevertheless, taurine supplementation improved the performance of freshwater fish such as rainbow trout (Gaylord et al. 2006, 2007), common carp (*Cyprinus carpio*; Abdel-Tawwab and Monier 2018) and Nile tilapia (*Oreochromis niloticus*; Al-Feky et al., 2015).

The grey mullet, which has attracted increasing interest as a promising candidate for aquaculture, is a catadromous species that spawns in taurine-rich seawater ecosystems and then commonly moves into less saline, taurine poor freshwater environments as juveniles. As

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a result, the aims of the current study were to (1) determine whether there is a specific dietary taurine requirement in juvenile grey mullet for enhanced growth and (2) the potential for taurine biosynthesis.

Materials and Methods

Experimental system

The experimental system consisted of sixteen 400- L V-tanks where UV treated, filtered (10 µm), ambient seawater (40 ‰) (computer controlled; Gavish, Israel) entered the bottom of the tanks and exited near the top through a 500 µm filter at a rate of 7 tank exchanges /day. This allowed the testing of 4 taurine 1 mm pelleted, non-fishmeal, omnivorous diets (0, 0.5, 1.0, and 2.0% DW diet) (Sparos Inc., Faro, Portugal) in replicates of 4 tanks/ treatment. The experimental system was exposed to a light intensity of 500 lux with a photoperiod of 11h light/13h dark. Each tank was stocked with 38 fish (126 dph; 7.32 ±0.44 g) and fed their respective diets at 4% tank biomass/day distributed over 5 rations. All fish were observed to finish their rations. The experiment continued for 58 days (184 dph), where the fish grew approximately 100%. At the end of this period, the weight and length of each fish were measured while 10 fish from each tank were sampled for fatty acid (3 fish) and taurine content of eyes, muscle, and liver (3 fish) as well as for RNA extraction from the livers (4 fish).

Fatty acid analysis

Fatty acid analysis was performed by chloroform-methanol (2:1) (Folch et al., 1957) extraction of total lipid from freeze-dried tissue samples (Gaon et al. 2021). The lipid-containing chloroform upper phase was removed and evaporated to dryness under a stream of nitrogen, and the total lipid was weighed (GH-120 analytical balance, A&D, San Jose, CA, USA). This was followed by adding the internal standard 17:0 (heptadecanoic acid; Sigma, St. Louis, MO, USA) to each sample. The samples were then transmethylated to their fatty acid methyl esters (FAME) by adding 1 mL/mg lipid of a 14% solution of boron trifluoride methanol (BF3) and sonicated for 1h at 50 °C. To the samples were added 0.5 mL double distilled water (DDW) and 1 mL/ mg lipid of analytical-grade hexane (99%), which was vortexed and then centrifuged (2300 rpm) for 2 min. The FAME was analyzed in a Varian 450–220 GC/MS/MS (Agilent Technologies, California, USA). Injected FAME samples (1 µL) were separated on a Varian WCOT fused silica column (50M ×0.32mm) at a flow rate of 1.5 mL/min and identified by known purified standards quantified using a response factor to the internal standard. The 30 min oven temperature program began at 70 °C for 4 min following injection and then increased to 300 °C at 10 °C/min for 3 min (Gaon et al. 2021).

Taurine analyses

This protocol was described by Koven et al. (2018). In brief, freeze-dried diet samples of 2–5 mg for taurine analysis on a Varian 325–410 HPLC (Agilent Technologies, California, USA) were prepared by adding 3 mL of 6 M HCL and 0.5% phenol. The samples were flushed with nitrogen and placed in a heating block for 24h at 108–110 °C. After cooling samples to room temperature and filtering (0.45 µm; cellulose nitrate), 0.5 mL carbonate buffer (pH 9), 0.5 mL DMSO (dimethyl sulfoxide), and 0.1 mL DNFB (1-fluoro-2,4 dinitrobenzene) were added, and the samples mixed well followed by heating for 15 min at 40 °C then cooled for 10 min. To the samples were added 6.5 mL of 0.01 M of buffered phosphate, vortexed for 30 s and then left to stand for 5 min. The samples were then transferred to HPLC vials and injected (10 µL) into an Acclaim ™120 C18 (5 µm, 4.6 × 150 mm) HPLC column (Thermo Scientific, USA). Column flow rate was 1.5 mL/min where specific ratios of buffer phosphate 0.01 M (pH 6) and acetonitrile (90;10, 10:90, 10:90, 90:10, 90:10) were introduced into the column at different times (0, 10, 11, 11.01, 18 min), respectively.

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RNA extraction

Total RNA was extracted from *Mugil cephalus* liver tissue by the guanidinium thiocyanate–phenol–chloroform extraction method (Chomczynski and Sacchi 1987) using Bio-Tri RNA reagent (Bio Lab Ltd., Jerusalem, Israel). The concentration of RNA was determined by measuring the absorbance at 260 nm in a spectrophotometer (Synergy HT, BioTek, Winooski, VT, USA). The purity of each sample was assessed for proteins by the 260 vs. 280 nm ratio. After residual DNA removal, a qScript™ cDNA Synthesis Kit (Quantabio, Beverly, MA, USA) was used to synthesize cDNA from RNA samples according to the manufacturer's protocol. Degenerate primers were designed for sequencing the desired genes. The PCRs were carried out in a final volume of 25 µL using the GoTaq® Green Master Mix (Promega, Madison, WI, USA) and 25 pmol of each Primer. PCR products were purified using a QIAquick PCR Purification Kit (QIAGENE, Hilden, Germany) and sequenced by Hy- Labs (Rehovot, Israel). Gene identity was confirmed by comparing the obtained sequences with those available at the Gene bank (http://www.ncbi.nlm.nih.gov/Genbank/). Real-time PCR was performed using PerfeCTa® SYBR® Green FastMix®, Low ROX™ (Quanta Biosciences, Inc. MD, USA). Gene-specific primers (**Table 2**) were designed and synthesized by Agentek (Tel Aviv, Israel).

A quantitative real-time polymerase chain reaction (qRT-PCR) was performed (in triplicates) in a total reaction volume of 10 µL, consisting of the respective primer sets (300 nM), cDNA template and PerfeCTa® SYBR® Green FastMix®, Low ROX™ (Quanta BioSciences, Inc. MD, USA). Since the fluorophore, Fast SYBR Green®, binds nonspecifically to double-strand DNA, it is necessary to ensure that the amplified PCR product is homogenous. Hence, the presence of a single amplicon was verified at the end of each run via a dissociation analysis (Melting curve), by which fluorescence was quantified regarding temperature rise. When the temperature increases, DNA strands separate, and the DNA bounded fluorophore releases. A single peak in a gaussian curve, which outlines the change in fluorescence as a function of temperature (-dF/dT), will indicate a homogenous PCR product.

To normalize the levels of target genes, qPCR for rRNA 18S was also performed with the sample cDNAs. A negative control with sterile water as the template was included to check for possible reagent contamination. Additionally, to rule out the presence of contaminating genomic DNA, our qPCR experiments included minus-reverse transcriptase controls (i.e., PCR amplification using DNAse-treated total RNA samples without reverse transcription as a template). The results were analyzed by 7500 Fast Real-Time PCR System software (Applied Biosystems, Waltham, Mass., USA). Gene expression levels were calculated using relative expression = 2-ΔΔCt, Ct – threshold cycle (Livak and Schmittgen 2001).

Statistics

Statistical analyses were performed using GraphPad Prism version 5.00 for Windows (GraphPad Software, San Diego, California, USA, www.graphpad.com). Growth (g) and fatty acid (mg/g DW tissue) values from the different taurine treatments are presented as mean ± SEM. Outliers were identified by calculating the Z value using the Grubbs test (Rousseeuw and Leroy, 2003) and removed if the calculated Z value was higher than the tabulated value. Every fish sampled for taurine and fatty acids in their liver, muscle, and eyes were considered a treatment replicate (3 fish sampled for liver, muscle, and eyes /treatment/ tank). Data values were analyzed by one-way ANOVA and Bartlett's test for equal variances. If significance (P <0.05) was found after ANOVA analysis while Bartlett's test was not significant (P > 0.05), then testing differences between groups were carried out by the Newman-Keuls Multiple Comparison tests. In cases where ANOVA and Bartlett's test were both significant (P < 0.05), then the non-parametric Kruskal-Wallis Test was applied, followed by Dunn's multiple comparison tests to determine significant (P<0.05) differences among treatments (Koven et al. 2018).

Ethics statement

All experimental animal procedures were conducted in compliance with the Guidelines of the European Union Council (86/609/EU) for the use of laboratory animals.

Results

The dietary ingredients, the content of indispensable amino acids, and the proximate analysis of the 4 taurine diet treatments, which showed no significant (P > 0.05) differences in macronutrient levels, appear in **Table 1a**, **1b**, and **1c**, respectively. **Table 2** lists the sense and antisense genetic primers for cysteine sulfinic acid decarboxylase (CSD), the rate-limiting enzyme in taurine synthesis, cysteamine (2-aminoethanethiol) dioxygenase (ADO), a key enzyme in an alternate pathway for taurine synthesis and cholesterol 7α hydroxylase (CYP7α1), the rate-limiting enzyme for bile salt synthesis.

Table 1 (a)The diet ingredients, (b) content of indispensable amino acids and the (c) proximate analysis (prox. anal.) of the 4 taurine diets; 0% (T0), 0.5% (T0.5), 1% (T1.0), and 2.0% (T2.0) taurine DW diet. In (a), the increasing dietary taurine levels[1] (% DW) were balanced by reducing equal percentages of whole wheat [2]. In (c), macronutrient levels between the diets having the same letter were not significantly (*P* > 0.05) different.

(a) Diet ingredients	% DW diet
Taurine[1]	0, 0.5, 1.0, 2.0
choline chloride	0.3
corn gluten	15
cornmeal	9
DCP	0.2
fish oil	5.5
poultry meal	13
rape seed	13
soy oil	5.5
soybean	12
dry Ulva	5
vit C-stay C	0.08
vitamin mix	0.3
wheat bran	13
wheat, whole[2]	8.12, 7.62, 7.12, 6.12
Total	100

(b) indispensable amino acids	% DW diet
Methionine	0.70±.00
Lysine	1.40±.01
Tryptophan	0.28±.02
Threonine	1.16±.04
Isoleucine	1.31±.08
Histidine	0.78±.02
Valine	1.62±.08
Leucine	3.13±.031
Phenylalanine	1.65±.009

(c) Prox. anal.	Taurine diets			
Diet components (%)	T0	T0.5	T1.0	T2.0
Protein	41.8^{a} ± 2.0	41.8^{a} ± 1.0	42.0^{a} ± 1.6	40.97^{a} ± 1.5
Lipid	15.7^{a} ± 0.2	13.8^{a} ± 0.9	14.4^{a} ± 0.2	14.67^{a} ± 1.1
Ash	10.1^{a} ± 0.7	9.7^{a} ± 0.2	10.2^{a} ± 0.7	9.71^{a} ± 0.2

Analyzed taurine dietary levels (0.05, 0.49, 1.0, 2.1% DW diet) differed markedly (P<0.05) from each other and matched theoretical values. Grey mullet juveniles exhibited significantly better average weight gain when fed a minimum of 0.5% taurine in the diet.

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Table 2 Gene-specific primer sets used for quantitative Real-time PCR for the genes cysteine sulfinic acid decarboxylase (CSD), cysteamine (2-aminoethanethiol) dioxygenase (ADO) and cholesterol 7α hydroxylase (CYP7α1)

Primer	Sense primer	Antisense primer
MC _18S	AGTTGGTGGAGCGATTTGTCT	ACGCCACTTGTGGCTCTAAGAAG
CYP7α	CCTCCCTGATAGAGACAATGGTG	CACCTTGTAGCAGAAAGCAAAGATG
CSD	CAGCCGCAAGGTGGACTG	CAAGCCAGCGGAGCCAAT
ADO	CGGCGTTCATGGATATCCTG	CCTTCGGCTCCGTGTTTTTC

In contrast, higher dietary levels of this nutrient did not elicit a better performance (**Figure 1a**). However, **Figure 1a** also demonstrated a higher but non-significant (P > 0.05) average FCR value for the control, which trended downwards with taurine supplementation. Additionally, the average Fulton condition indexes (CI), specific growth rate (SGR), and relative growth rates (RGR) were not statistically different for all treatments (P>0.05) in **Figure 1b**, **1c**, and **1d**, respectively.

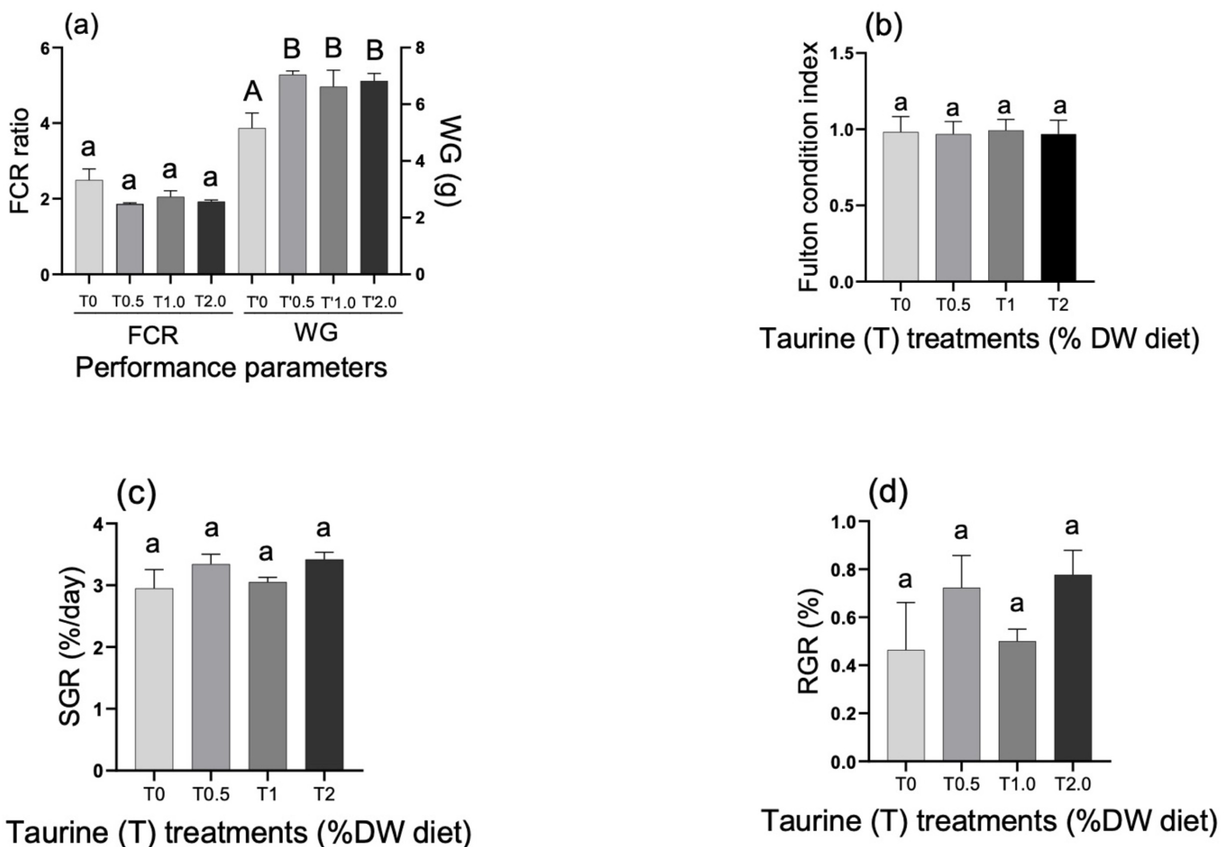

Figure 1 The effect of the taurine diets T0, T0.5, T1.0, and T2.0 (0, 0.5, 1.0, and 2.0% taurine DW diet, respectively) on growth parameters; (a) average FCR (food conversion ratio) and WG (weight gain) /treatment as well as (b) average Fulton condition index, Specific growth rate (SGR) and Relative Growth Rate (RGR)/treatment. Bar values ± SEM, within a performance parameter having different letters, were significantly (P < 0.05) different.

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Nevertheless, fish fed the taurine diets demonstrated populations with a markedly (*P* < 0.05) higher average number of surviving fish (23.4±1.1) of moderately sized (10-20 g) cohorts than smaller (< 10 g) individuals (12.5±1.1). In contrast, the fish fed the taurine control (0% taurine supplementation) exhibited similar average numbers of small and moderate-sized fish (18.0±3.6-20.0±4.1) (**Figure 2**). All treatments demonstrated significantly (*P*<0.05) lower average numbers of large (>20 g) surviving fish (**Figure 2**).

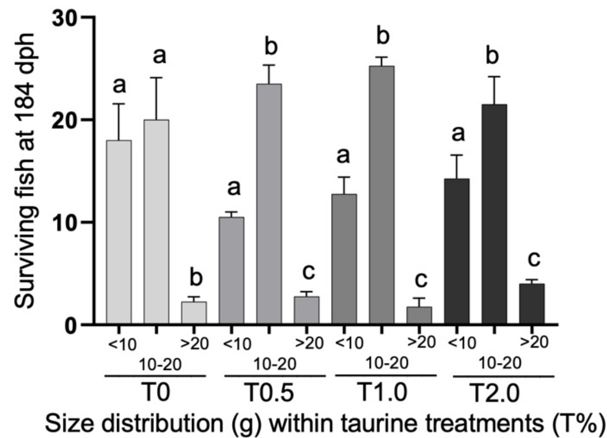

Figure 2 The effect of the dietary taurine treatments (T0, T0.5, T1.0, and T2.0% of DW diet) on size distribution (<10, 10-20, >20 g) of surviving fish/treatment at the end of the feeding trial (184 dph). Treatment bar values (± SEM) within a treatment having a different letter were significantly (*P* < 0.05) different.

Figure 3 showed that taurine significantly (P<0.05) accumulated in the liver, eyes, and muscles. Moreover, muscle taurine markedly (P<0.05) increased in a dietary taurine dose-dependent manner and accumulated up to 5.0 and 4.8 times more taurine than the liver and eyes, respectively (**Figure 3**). However, there was no significant (P<0.05) effect of the taurine diets on the main fatty acid classes; saturated, monounsaturated, and polyunsaturated fatty acids in the eyes, liver, and muscle tissue (**Table 3**).

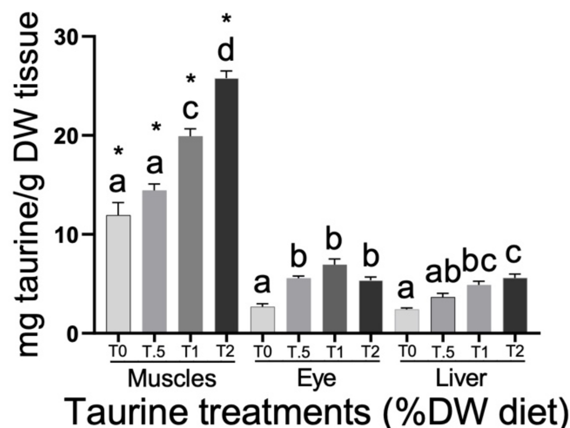

Figure 3 The effect of dietary taurine treatments (0, 0.5, 1.0, and 2.0% DW diet) on the taurine accumulation in the muscles, eyes, and liver of juvenile grey mullet at the end of the study. Taurine bar values ± SEM within muscle, eyes, and liver tissues having different letters were significantly (*P* < 0.05) different. Muscle taurine bar values having an asterisk were significantly (*P* < 0.05) higher than taurine bar values of the same treatment in the eyes and liver.

Table 3 The effect of dietary taurine (T) treatments (0, 0.5, 1.0, and 2.0% DW diet) on saturated, monounsaturated, and polyunsaturated fatty acid classes in the eyes, liver, and muscle tissues. No significant (*P*>0.05) quantitative differences of the main fatty acid classes, as a function of dietary taurine level, were found

Tissue	*Fatty acid class (mg/g DW)*	*Taurine treatments (%)*			
		T0	T0.5	T1.0	T2.0
Eyes	saturates	40.8 ± 2.2	45.0 ± 2.8	41.7 ± 2.5	41.9± 2.3
	monounsaturated	43.8 ± 4.9	54.9 ± 3.9	53.4 ± 3.7	51.5 ± 2.9
	polyunsaturated	30.5 ± 4.7	36.1 ± 6.1	44.1 ± 6.6	35.3 ± 5.0
Liver	saturates	35.6 ± 4.7	33.9 ± 2.4	30.6 ± 2.9	36.1 ± 3.4
	monounsaturated	48.1 ± 6.9	50.7 ± 4.9	41.9 ± 4.0	50.1 ± 5.2
	polyunsaturated	17.9 ± 3.4	24.3 ± 2.3	17.1 ± 1.33	22.1 ± 2.3
Muscle	saturates	46.1 ± 3.6	38.1 ± 3.9	41.0 ± 4.3	44.9 ± 3.8
	monounsaturated	62.4 ± 3.5	56.6 ± 6.5	60.2 ± 7.9	69.5 ± 3.8
	polyunsaturated	18.2 ± 1.7	17.2 ± 2.2	17.8 ± 2.6	21.1 ± 3.4

The gene expression of liver CSD exhibited a significant (P<0.05) upregulation with increasing dietary taurine from the control to 1% taurine DW diet but was downregulated (P<0.05) in fish fed the 2% taurine diet (**Figure 4a**). On the other hand. There was very low detectable gene expression associated with dietary taurine in the transcription of ADO, a key enzyme in the cysteamine alternate taurine synthesis pathway (**Figure 4b**). Although there was minor gene expression of the rate-limiting enzyme in bile salt synthesis (CYP7α1), there was no discernible effect of dietary taurine (**Figure 4c**).

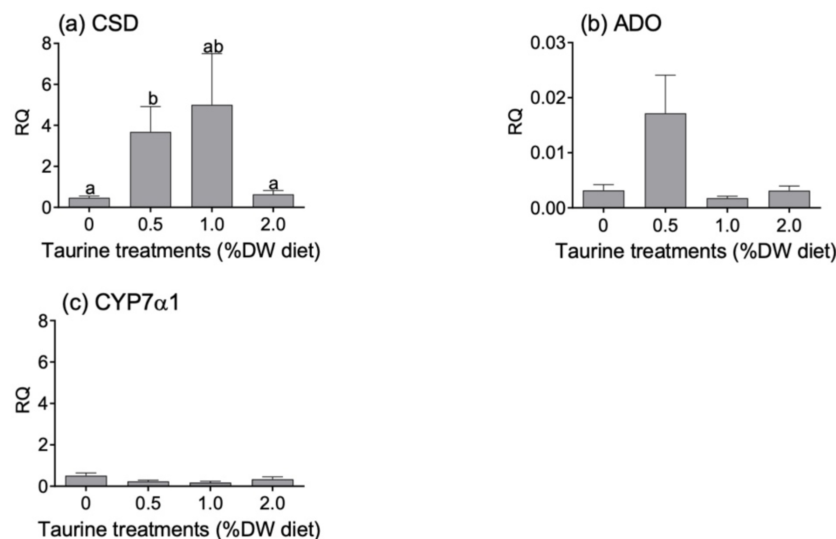

Figure 4 The effect of dietary taurine (T) treatments (0, 0.5, 1.0, and 2.0% DW diet) on the gene expression of (a) cysteine sulfinic acid decarboxylase (CSD), (b) cysteamine (2-aminoethanethiol) dioxygenase (ADO) and CYP7α1 in juvenile fish. Bars values (± SEM) having a different letter(s) were significantly (*P* < 0.05) different.

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Discussion

The results of this study demonstrated that supplementing the diet with 0.5% taurine (DW diet) significantly improved growth, whereas higher dietary taurine provided no added benefit. However, the low overall weight gain was somewhat surprising and suggested that the growth-promoting effect of taurine supplementation in omnivorous juveniles appears to wane compared with its carnivorous larval stage and larvae from other species (Salze et al. 2012; Kim et al. 2016). Nevertheless, taurine supplementation resulted in a higher percentage of larger mullet in the population compared to the control 0% taurine treatment. The growth-promoting effect of dietary taurine has been well documented in the Japanese flounder (Park et al. 2002), European sea bass (*Dicentrarchus labrax*; Brotons Martinez et al. 2004), yellowtail (Matsunari et al. 2005), juvenile cobia (*Rachycentron* canadum; Lunger et al. 2007) and golden pompano (*Trachinotus ov*atus; Wu et al. 2015).

The dietary taurine requirement in teleosts is generally due to a deficiency in cysteine sulfinic decarboxylase (CSD), the rate limiting enzyme for taurine synthesis (Goto et al. 2003). Broadly speaking, taurine synthesis and CSD activity differ among fresh and seawater fish. Marine fish species, such as Japanese flounder, red sea bream and yellowtail, demonstrated a lack of taurine synthesis capability as CSD activity is absent or at negligible levels (Kim et al. 2008). This means that in aquaculture, taurine must be provided in the diet, particularly if the food has been supplemented with plant-based meals, which are devoid of taurine (El Sayed 2014). On the other hand, freshwater teleosts, such as rainbow trout, Atlantic salmon and common carp can synthesize taurine (Kim et al. 2008). This was shown when taurine tissue concentrations increased with methionine and cystine supplementation, which are precursors for taurine synthesis. (Yokoyama and Nakazoe 1992). Nevertheless, the levels of endogenous CSD activity reported in rainbow trout and tilapia (Yokoyama et al. 2001) were considered insufficient as dietary taurine was still required for good growth (Gaylord et al. 2006). Lunger et al. (2007) reasoned that although cobia could synthesize taurine from sulfur containing amino acids, dietary taurine supplementation spared the metabolism of the essential methionine and tryptophan amino acids, which could then be channeled to other critical physiological processes that promote growth. In contrast, Kim et al. (2008) concluded that the common carp doesn’t appear to have a dietary taurine requirement as they have significant taurine biosynthesis capability putatively through the cysteamine dioxygenase pathway (ADO) and not the CSD pathway (Gonzales-Plasus et al. 2019). However, the present study clearly demonstrated almost undetectable gene expression. This suggests that this pathway made little or no contribution to endogenous taurine synthesis, compared to the CSD pathway in grey mullet juveniles, which has also been reported in mammals (Saltz and Davis 2015).

Although liver CSD activity was not directly measured, the gene expression for liver CSD protein was impressively upregulated 7.8x and 10.6x in the 0.5% and 1.0% taurine fish, respectively, compared to the 0% taurine fish. This indicated that juvenile grey mullet adopts the freshwater model and exhibits taurine synthesis capability. Moreover, the salinity decrease wouldn’t be a trigger when mullets are migrating to lower saline, estuarine waters as this study was conducted at 40 ‰. However, as in other freshwater species, the endogenously produced taurine appears to fall short of completely satisfying the mullet requirement, as evidenced by the significantly improved growth of fish feeding on the 0.5% taurine diet.

Although CSD gene expression significantly increased in the liver of mullet fed taurine supplemented diets up to 1.0%, this gene was down regulated in fish fed the 2% taurine diet. This seems counter-intuitive as the question arises why would fish synthesize taurine if they are receiving it in the diet? Similarly, Goto, et al. (2004) feeding diets containing different taurine levels to freshwater bluegill (*Lepomis macrochirus*), found that that CSD activity increased with dietary taurine level.

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A possible explanation may be linked to the important role of taurine as an osmolyte, which has been reported in a range of marine species such as flounder (*Pseudopleuronectes americanus*; King et al. 1982) and skate (*Raja erinacea*; Ballatori and Boyer 1992) as well as freshwater fish such as walking catfish (*Clarias batrachus*; Saha et al. 2000), tilapia and carp (Takeuchi et al. 2000a, b). The increased taurine in the blood circulation of mullet juveniles consuming higher dietary taurine levels, may have stimulated taurine synthesis in liver cells to reduce osmotic difference across the tissue membranes. This would prevent cell shrinkage as well as changes to the intracellular hydromineral balance. Taurine has been described as a critical osmolyte in mammalian tissues (Pasantes-Morales et al. 1998). Studies on brain and neuron cells in mice and rats have shown changes in inorganic ions and taurine as mechanisms to maintain cell volume in response to osmolyte changes in plasma (Pasantes-Morales et al. 1993). Taurine is better suited than other ions for volume regulation in the brain and neural tissue as large ion fluxes affect the transmembrane potential and potentially induce action potentials (Garg et al. 2011). The cell taurine content of brain astrocyte primary cultures increased with extracellular taurine concentration through endogenous synthesis via the CSD pathway (Reymond et al. 1996).

In contrast, Bitoun and Tappaz (2000), working on brain astrocyte cells, argued that taurine synthesis would be insufficient to explain intracellular taurine content and is likely accompanied by the biosynthesis of taurine transporters (TauT). This would allow more extracellular taurine to enter the cell. An increase in TauT synthesis may explain the sharp decrease in CSD gene expression in the 2% taurine diet. The switching to enhanced transport of taurine into the cell may be more energy cost-effective than intracellular biosynthesis as a strategy to combat shell shrinkage and osmotic challenges in fish fed high taurine supplemented diet.

It is well documented that taurine also plays a major role in forming bile salts, which is essential for intestinal digestion and absorption of lipids (Koven et al. 2016). These authors demonstrated that dietary taurine increased total lipid and all fatty acid classes in the eye tissue of white grouper (Epinephelus aeneus), which may have improved vision and feeding behavior. However, in this study, there was no dietary taurine dose-dependent effect on the levels of fatty acid groups (saturated, monounsaturated, or polyunsaturated fatty acids) in the eyes, liver, or muscle. This suggests that the endogenous taurine synthesis may have been sufficient to produce adequate bile salts to emulsify ingested lipids. In support of this, the gene expression of cholesterol 7α-hydroxylase (CYP7α1), the rate-limiting enzyme in bile salt synthesis, was independent of dietary taurine in this study and displayed very low expression levels.

Taurine accumulated in the eyes, liver, and muscles in a dietary dose-dependent manner but was markedly higher in the muscles. Taurine muscle accumulation correlated strongly with dietary taurine even though growth performance didn't improve over the 0.5% dietary inclusion level. The higher accumulation of taurine in the muscles compared to the liver and eyes has been observed in juvenile turbot (*Scophthalmus maximus* L.) (Qi et al. 2012), white grouper (Koven et al. 2016) and mice (Ito et al. 2014). Taurine represents 30-50% of the free amino acid pool in animal and fish's blood, muscles, and brains (Saha et al. 2000, 2002). It is an important modulator of muscle contractile function through the regulation of ion movement, osmoregulation, and oxidative stress (Schaffer et al. 2000, 2009) as well as stimulating muscle hyperplasia (Sampath et al. 2020) and modulating energy metabolism (Wen et al. 2018). All these factors may directly or indirectly promote growth. On the other hand, this study's suggested endogenous synthesis of taurine may have muted a stronger dietary contribution by this nutrient to muscle accretion. Nevertheless, there is a broad agreement between these results with the taurine requirement for good growth in other species such as turbot (Qi et al., 2012), yellowtail (Matsunari et al., 2005), Japanese flounder (Kim et al. 2007) and red sea bream (Matsunari et al. 2008a, b).

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Interestingly, Qi et al. (2012) suggested that fish size determined the response and requirement for dietary taurine. In support of this, Kuzmina et al. (2008) proposed that the polyfunctionality of taurine would vary with fish size and developmental stage, potentially leading to a variable requirement for this nutrient. This is consistent with our observations that carnivorous grey mullet larvae appear to have a stronger taurine requirement (Koven, pers. Communication) than the omnivorous juvenile mullet in the present study.

In summary, dietary taurine accumulates in juvenile grey mullet eyes, liver and muscle tissues in a dose-dependent manner but demonstrated a specific requirement for improved growth only at the 0.5% dietary level. Juvenile mullet exhibited increased CSD gene expression, suggesting taurine synthesis capability in the liver. However, this endogenous taurine production was not channeled into increased bile salt synthesis and subsequent fatty acid digestion and absorption. Instead, taurine may have been mainly used in fish fed 0.5 and 1% taurine as an osmolyte in liver tissue to reduce the cellular osmotic gradient with the blood to maintain cell volume and hydromineral balance. Moreover, endogenous taurine synthesis was not triggered by a reduction in salinity as this study was conducted entirely in the Red Sea's ambient seawater (40 ‰). This implies that mullet taurine synthesis capability is more likely a function of development from carnivorous larvae to omnivorous juveniles.

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