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REVIEW

Roles of dietary taurine in fish nutrition

W. W. H. A. Sampath[1,2,3] · **R. M. D. S. Rathnayake**[4] · **Mengxi Yang**[1,2,3] · **Wenbing Zhang**[1,2,3,5] · **Kangsen Mai**[1,2,3,5]

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Abstract
Taurine is a conditionally essential amino acid in fish nutrition. The present study addressed the practical application of examining published data on fish nutrition over the past 20 years, emphasizing the topic of taurine by using computational tools and their applications. According to the published articles, an increased linear growth of research occurred, with Japanese flounder being the most examined fish species. Dietary taurine supplementation has several beneficial effects in fish nutrition, such as survival, growth, feed utilization, protein and energy retention, intermediate metabolism, anti-oxidation, anti-stress, disease resistance, muscle texture and reproductive performance. Also, there are negative effects in some species. Dietary taurine exerted effects on several gene expressions and enzyme activities; these are important in taurine metabolism in fish. These genes and enzymes included taurine transporter (TauT), cysteine dioxygenase (CDO), cysteamine dioxygenase (ADO), cysteine sulfonate decarboxylase (CSD) and pretrypsinogen (Ptry). Plant protein-based diets with taurine supplementation are recommended because of the absence of taurine in plant protein.

Keywords Taurine · Fish · Amino acid · Nutrition · Feed

Introduction

As the world's population increases, aquaculture plays an important role in meeting the high demand for fish products (Magalhães et al. 2019). Increasing demand, uncertain availability and the high price of fish meal lead to a drive to find alternative protein sources to reduce dependency on fish meal as the main protein source in aquafeeds. Plant proteins are formulated as the main fish meal substitutes in fish feed. However, there are some nutritional imbalances when dietary fish meal is replaced by plant protein source (Castillo and Gatlin 2015). Taurine is an amino acid that is abundant in fish meal, but limited in plant protein sources. Normally in fish, taurine is synthesized in liver. However, some fish species have a limited ability to synthesize taurine (Wei et al. 2018). Taurine has been identified as an essential amino acid in several fish species, notably in juvenile and larval stages (Salze and Davis 2015). As an example, taurine is an essential nutrient in Nile tilapia (*Oreochromis niloticus*) (Al-Feky et al. 2016a, b), Japanese flounder (*Paralichthys olivaceus*) (Han et al. 2014) and Senegalese sole (*Solea senegalensis*) (Pinto et al. 2010). Some fish species require dietary taurine supplementation due to a reduced ability to biosynthesize taurine inside their body (El-Sayed 2013). Several studies have shown increased growth performance and feed efficiency of fish fed low fish meal diet with taurine supplementation (Magalhães et al. 2019; Sampath et al. 2020; Zhang et al. 2018). Taurine and trimethyl taurine (TMT) exert different effects on protein metabolism, although they have similar structures. In principle, they create hydrogen bonds with surface proton donor groups, which do not directly interact with proteins (Bruździak et al. 2018). L-Cysteine is converted into taurine after the process

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✉ Wenbing Zhang
wzhang@ouc.edu.cn

[1] The Key Laboratory of Aquaculture Nutrition and Feeds, Ministry of Agriculture and Rural Affairs, Qingdao 266003, China

[2] The Key Laboratory of Mariculture, Ministry of Education, Qingdao 266003, China

[3] Ocean University of China, Qingdao 266003, China

[4] Developmental Molecular Biology Laboratory, Ocean University of China, Qingdao 266003, China

[5] Laboratory for Marine Fisheries Science and Food Production Process, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, China

of oxidative enzymatic action in the biosynthesis process (Liu et al. 2017). Taurine synthesis is regulated mainly by taurine biosynthesis enzymes and taurine transporter (TauT). Enzymes involved in the oxidation process affect the efficiency of taurine synthesis from cysteine. TauT transports taurine from the cell plasma to mitochondria (Schuller-Levis and Park 2003). Dietary sulfur-containing amino acids stimulated the taurine biosynthesis process in rainbow trout (Wang et al. 2016).

Several studies have shown the effects of taurine nutrition and deficiency. Dietary taurine supplementation resulted in increased total protein content and alkaline phosphatase activity in plasma, and glutathione reductase activity and heat-shock protein (HSP70) content in liver and reduced blood cell apoptosis (Tan et al. 2018). Also, taurine is an important nutrient in broodstock, larval and juvenile fish nutrition (Sarih et al. 2019). Moreover, taurine is involved in bile acid conjugation, cell membrane stabilization, osmoregulation and anti-inflammatory events (Moura et al. 2018). In addition, it affects cell proliferation, and hence it has a direct correlation with muscle growth (Wang et al. 2016; Wen et al. 2018). Taurine deficiency may cause a high requirement of vitamin C and vitamin E in marine fish larvae (Izquierdo et al. 2019). Taurine deficiency may lead to poor growth performance, green liver syndrome and psychological abnormalities of fish fed with fish meal-free diets (Takagi et al. 2008). Moreover, there are many primary responses of fish that have been identified involving dietary taurine supplementation and include survival rate (Rotman et al. 2017), growth performance (Poppi et al. 2018; Zhang et al. 2018), feed utilization (Al-Feky et al. 2016b; Ferreira et al. 2014; Peterson and Li 2018; Salze et al. 2018b; Satriyo et al. 2017), body composition (Hernandez et al. 2018; Hoseini et al. 2017), whole body taurine (Hoseini et al. 2018; Salze et al. 2018a; Stuart et al. 2018), anti-oxidative capacity (Abdel-Tawwab and Monier 2018; Zhang et al. 2018), immune response (Khaoian et al. 2014; Kim et al. 2017; Koven et al. 2016; López et al. 2015; Nguyen et al. 2015; Richard et al. 2017; Zhang et al. 2019), cellular and metabolic responses (Feidantsis et al. 2014), hyperplasia muscle growth (Sampath et al. 2020), egg fertilization (Sarih et al. 2019) and reproductive performance (Al-Feky et al. 2016a; Guimaraes et al. 2018). Taurine is a vital ingredient in fish nutrition, especially when feeding with plant protein-based diets. Fish meal is considered as the most adequate protein source in fish feed. However, plant protein-based feeds have been used in industry, but there are some limitations in nutritional content. Partial replacement of fish meal with taurine in fish feed can reduce feed cost as well as improve the growth performance in fish. So, taurine is an important nutrient in fish feed formulae, especially concerning carnivorous fish (Zhang et al. 2019). The scientifically proven benefits of dietary supplementation of taurine in fish nutrition research have been published mostly after 2000. Taurine has a wide range of benefits in fish nutrition. Moreover, the roles of taurine in different life and reproductive stages have not been widely investigated. The present study has focused on the roles of dietary taurine in fish nutrition by using a comprehensive analysis of 20 years of published research data. The study includes the optimum taurine supplementation level, optimum life stage to supplement the taurine in feed formulae, the fish species which have the most significant impact and the roles of the *TauT* gene in taurine synthesis. Furthermore, the present study concludes the roles of taurine in different fish species, life stages, habitat, the primary protein source in feed, the inclusion of fish meal and the primary function of taurine. The nutritional importance of taurine in fish nutrition, and how it affects nutritional metabolism and functions of the fish are also investigated.

Methodology

In the present study, published data after the year 2000 relating to dietary taurine roles in fish nutrition were analyzed and visualized by using a computational literature mining model. Literature text mining techniques have been widely used in bioinformatics and biomedical research due to the high efficiency of literature capture in any specific topic. The present study collected research data from data mining and filtering by "rentrez", R package according to the title of the article, fish species, life stages, taurine supplementation and primary response (Winter 2017). Then, the collected data were carefully summarized and tabulated for analysis and visualization. Genetic databases including the National Center for Biotechnology (NCBI) gene database were used to collect gene frequencies of the *TauT* gene in different fish species (Lamurias and Couto 2019). To calculate the optimum dietary supplementation level, all the taurine data were entered separately and tabulated. Tabulated data were filtered to make graphs and figures. The data were expressed as mean ± SEM (standard error of the mean) and analyzed by one-way analysis of variance (ANOVA) using SPSS 23.0. The number of times taurine supplementation used according to fish species and taurine levels was visualized by using Tableau Desktop 2020.1. Articles were summarized according to fish species, life stages, living environment of the fish, best-recommended taurine level, with or without fishmeal, the primary response and the main protein sources in the diet. Also, the synergic effects of different nutrients with taurine were studied.

Properties and biosynthesis of taurine

The full chemical name of taurine is 2-aminomethane sulfonic acid. It is converted from L-cysteine after the process of oxidative enzymatic action in the biosynthesis processes in liver (Liu et al. 2017). In 1827, taurine was isolated initially by Leopold Gmelin and Friedrich Tiedemann (Seidel et al. 2018). It was originally found in bile acids of the ox (*Bostaurus*) and the name was derived from *Taurus*. As a sulfur-containing amino acid, taurine is highly abundant in most animal tissues, especially in marine animals. Plant and fungi contain very low concentrations (Sundararajan et al. 2014). Taurine is commonly found in muscle, brain, liver and kidney, and it helps to develop the functions of skeletal muscles, cardiovascular and central nervous systems, and the retina (Onsri and Srisawat 2016). In fish, taurine is synthesized in liver from methionine and cysteine. However, the ability of biosynthesis varies according to fish species. Also, it has been highlighted that taurine deficiency leads to certain inferior performance and physiological abnormalities (Shen et al. 2018). Taurine is generally considered as an essential amino acid for fish. It is required in primary situations when production is decreasing due to deficiencies or lack of ability to synthesize taurine in liver (El-Sayed 2013).

Taurine affects proteins because it has the main ability of directly interacting via an amine (NH_3^+) group (Bruździak et al. 2018). Taurine is involved in several metabolic pathways, such as methionine metabolism (Andersen et al. 2015), bile acid biosynthesis (Salze and Davis 2015), inner membrane transport (Luirink et al. 2005) and sulfur metabolism (Liu et al. 1994). It has many functions, such as bile acid synthesis, cell volume regulation, cytoprotection of the central nerve system and modulation of intracellular calcium (Ripps and Shen 2012). Normally, methionine-derived homocysteine is a sulfur source, and its condensation products with serine are converted into cysteine in animals. The major pathway of taurine biosynthesis includes several sequences of the oxidation process. Cysteine is converted into cysteine sulfinic acid by cysteine dioxygenase (CDO), and then hypotaurine is produced by cysteine sulfinic acid by cysteine sulfonate decarboxylase (CSD) followed by hypotaurine dehydrogenase and produce taurine (Fig. 1). CDO regulates the cysteine concentration, and CSD enzyme is the rate-limiting step in taurine biosynthesis. CDO and CSD are the key enzymes in the taurine biosynthesis process in the liver (Wang et al. 2014). Moreover, a membrane transporter of taurine has a critical role for transport and recycling of taurine. However, regulation of taurine biosynthesis differs according to the fish species because of the key enzyme activities, especially CDO and CSD. Those enzyme activities depend on the osmotic conditions, ontogenetic stages, hormone status and diet formulation. Taurine biosynthesis is higher in rainbow trout than Japanese flounder (Wang et al. 2016). Taurine is synthesized through a transsulfuration pathway by using aspartate aminotransferase by some freshwater fish species, such as rainbow trout and common carp (Guimaraes et al. 2018). However, the taurine biosynthesis pathway in fish is still poorly described in the literature (Salze and Davis 2015). The addition of taurine to zebrafish (*Danio rerio*) liver cells grown in taurine-free medium has little effect on transcription levels of the biosynthetic pathway genes for cysteine dioxygenase (CDO), cysteine sulfonate decarboxylase (CSAD) or cysteamine dioxygenase (ADO). In contrast, supplementation with taurine causes a 30% reduction in transcription levels of

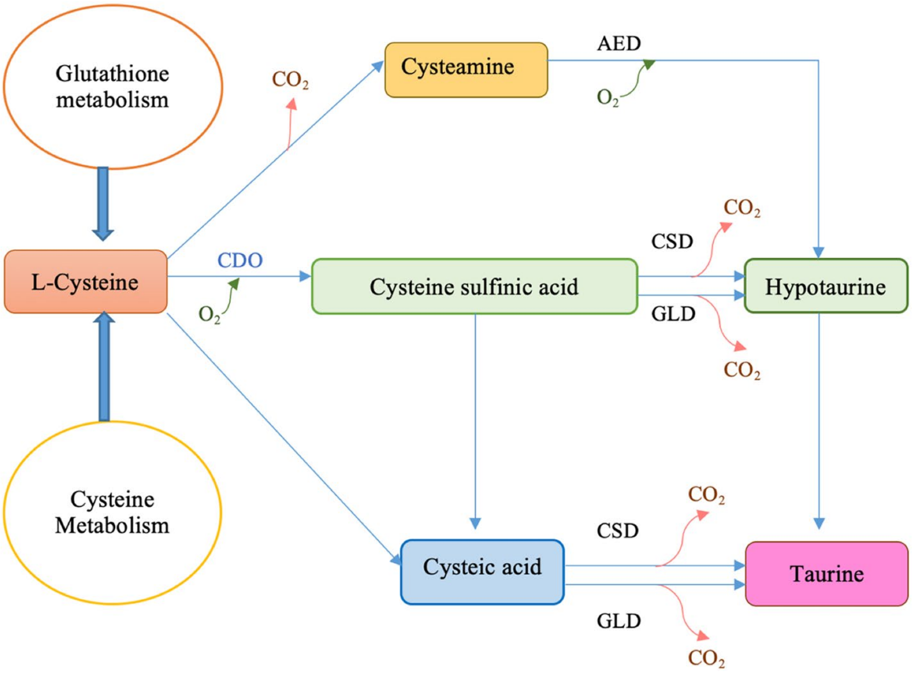


Fig. 1 Taurine biosynthesis pathway. (Source: KEGG pathway map-00430, Liu et al. 2017). *CDO* cysteine dioxygenase type 1, *CSD* cysteine sulfonate decarboxylase, *GLD* glutamate decarboxylate, *AED* 2-aminoethanethiol dioxygenase

the taurine transporter, TauT. The importance of taurine to *TauT* gene expression in liver has been confirmed (Liu et al. 2017).

Low or absence of CSD activity in liver could lead to a lack or low capacity of taurine synthesis, especially in the juvenile stage of fish (Martins et al. 2018). Hepatic taurine concentration was marginally increased with the growth of rainbow trout. Furthermore, mRNA and CSD levels were dramatically increased with the growth of rainbow trout (Wang et al. 2015). Dietary sulfur amino acids, such as methionine and cysteine, stimulated taurine biosynthesis with increased hepatic CDO and liver taurine concentration, but not significantly affected the hepatic CSD activities in turbot (*Psetta maxima*) (Wang et al. 2014). Carnivorous fish have a lower capacity of taurine biosynthesis than herbivorous fish. Supplementation of dietary taurine increases the utilization of plant protein in carnivorous fish (Zhang et al. 2018). So, taurine improves the growth performance of several carnivorous fish, including turbot (*Scophthalmus maximus*) (Liu et al. 2018; Wei et al. 2018; Zhang et al. 2019), red sea bream (*Pagrus major*) (Takagi et al. 2010), Japanese flounder (*P. olivaceus*) (Kim et al. 2017) and yellowtail (*Seriola quinqueradiata*) (Khaoian et al. 2014; Nguyen et al. 2015). Therefore, taurine is a vital nutrient for the abovementioned fish species especially in their rapid growth stage, where most CSD actions take place in the liver. So, all those properties are vitally important factors in fish nutrition.

Statistical analysis of research on fish taurine nutrition

According to the data set, more than 100 specific queries of the literature were tabulated. The research trend line was with $R^2 = 0.46$, and P value $= 0.0018$. A linear trend model is computed for the sum of the number of records given published years. The literature number was significantly increased by the year ($P < 0.05$). The maximum number was recorded in the year 2018 with 18 records, and the minimum number was recorded with one record in the year 2001, 2002, 2009 and 2010, respectively. There was a trend line of significantly increasing number of articles in the special field of taurine supplementation and metabolism because of the increase of research, funding, high demand of seafood as a protein source, limitation and the high price of fishmeal, an increasing number of concerns on taurine, and the previous research motivations. Japanese flounder (*P. olivaceus*) was the most studied fish species, followed by red sea bream, yellowtail and turbot. The numerous positive effects with few negative effects of dietary taurine supplementation on growth and metabolism in fish were recorded (Table 1). Further research is needed on certain fish and their different life stages to clarify the role of taurine and its nutritional value for other nutrient metabolism.

Growth performance

In most of the published studies, the positive effects of dietary taurine supplementation on the growth and feed utilization of fish were found, especially for the fish fed with plant protein-based diets. These fish species include white seabream (*Diplodus sargus*) (Magalhães et al. 2019), turbot (Liu et al. 2018; Sampath et al. 2020; Wei et al. 2018; Zhang et al. 2019), rock bream (*Oplegnathus fasciatus*) (Ferreira et al. 2014), common carp (*Cyprinus carpio*) (Abdel-Tawwab and Monier 2017), snapper (*Lutjanus colorado*) (Hernandez et al. 2018), black carp (*Mylopharyngodon piceus*) (Zhang et al. 2018) and channel catfish (Peterson and Li 2018). Furthermore, it was found that dietary methionine supplementation was inefficient in the plant-based diets to overcome the taurine deficiency for the growth performance of meagre (*Argyrosomus regius*). So, taurine supplementation is necessary for plant protein-based diets (Moura et al. 2018).

However, the nonresponse or negative effects of dietary taurine supplementation on fish were also found in some previous studies. Growth and feed utilization of barramundi (*Lates calcarifer*) were not significantly affected by taurine supplementation of the plant-based diets with 1.5% of the final taurine content (Poppi et al. 2018). Also, Kato et al. (2014) found no significant difference in growth, survival, feed intake and feed efficiency of red sea bream fed with or without taurine-supplemented diet. No significant effects of dietary taurine supplementation on growth performance were found in some other fish species, such as grass carp (Yang et al. 2013) and yellowtail (Khaoian et al. 2014). Furthermore, Hoseini et al. (2017) found negative effects on the growth performance of juvenile Persian sturgeon (*Acipenser persicus*) fed with taurine-supplemented diet compared to the controls without taurine supplementation. The similar negative results were found in Persian sturgeon (*A. persicus*) (Hoseini et al. 2017) and European sea bass (*Dicentrarchus labrax*) (Coutinho et al. 2017).

Based on the positive effects of dietary taurine supplementation, the results of most research suggested that optimal dietary taurine content was between 0.5 and 1.5%, whereas 1% was the most recorded value (Fig. 2). According to the data set, the statistically optimal content of dietary taurine for the growth and metabolism of fish was 0.91 ± 0.06% (the mean value) (Fig. 3). Among published articles, the juvenile stage was the most tested life stage of the fish. Some deviations from the statistically optimal dietary taurine content were observed because of the specific experimental conditions and different life stages of fish. So, even with the same fish species, the optimum taurine level has deviated according to the life stages, feed formula and the experimental conditions. Also, it has been suggested that optimum taurine level is a species-specific factor for

Table 1 Summary of dietary taurine supplementation for different species and life stages of the fish

Common name	Scientific name	Life stage	Living environment	Initial BW (g)	Primary protein source(s)	W or WO FM	Tau%	Function(s)	References
Amberjack	*Seriola dumerili*	Adult	Marine water	11.99	FM, Wheat, WG	W	1.1	Egg fertilization	Sarih et al. (2019)
Barramundi	*Lates calcarifer*	Juvenile	Marine water	26.8	SPC, FM	W	0.547	Growth	Poppi et al. (2018)
Black carp	*Mylopharyngodon piceus*	Juvenile	Fresh water	5.94	SBM, CSM, SFM	W	0.1	Growth, enzyme activity, antioxidant status	Zhang et al. (2018)
California yellowtail	*Seriola lalandi*	Juvenile	Marine water	4.89	WW, PBM, SBM, SPC	WO	0.26	Growth, feed intake (FI), feed efficiency (FE), Tau deposition, protein deposition	Salze et al. (2018b)
		Larvae	Marine water	1	SQM, KM	WO	NA	Growth, survival, whole body taurine	Stuart et al. (2018)
		Larvae	Marine water	NA	Ritifers (larval feed)	WO	NA	Survival	Rotman et al. (2017)
Channel catfish	*Ictalurus punctatus*	Juvenile	Fresh water	5.6	SBM, CSM	WO	0.2	Growth, feed efficiency	Peterson and Li (2018)
Cobia	*Rachycentron canadum*	Juvenile	Marine water	10	FM, CPC, PBM, SBM	W	0.44	Growth, feed efficiency, TauT gene expression	Watson et al. (2014)
		Juvenile	Marine water	NA	SPC, CG, SBMse	WO	1.5	Growth	Watson et al. (2013)
Common carp	*Cyprinus carpio*	Larvae	Fresh water	0.97	SBM, CF, FM	W	1.5	Growth, enzyme activity, antioxidant capacity (AOC), tolerance	Abdel-Tawwab and Monier (2017)
European sea bass	*Dicentrarchus labrax*	Juvenile	Marine water	15	SPC, SBM	WO	5	Retinal anatomy and function	Brill et al. (2019)
				55	SBM, FM	W	0.7	Growth, feed efficiency, protein efficiency ratio	Martins et al. (2018)
				6.9	FM	W	1	Growth, oxidative response	Coutinho et al. (2017)
				85	FM, SPC, CG	W	0.2	Cellular and metabolic response	Feidantsis et al. (2014)
Florida pompano	*Trachinotus carolinus*	Juvenile	Marine water	7.73	SBM, WW, PBM	WO	0.25	Growth, feed efficiency, whole body taurine	Salze et al. (2018a)
Gilthead seabream	*Sparus aurata*	Larvae	Marine water	0.121	SQP	WO	0.71	Growth, survival, anti-oxidative enzymes	Izquierdo et al. (2019)
Golden pompano	*Trachinotus ovatus*	Juvenile	Marine water	14.3	SPC, SBM, PBM, FM	W	0.5	Growth	Wu et al. (2015)

Table 1 (continued)

Common name	Scientific name	Life stage	Living environment	Initial BW (g)	Primary protein source(s)	W or WO FM	Tau%	Function(s)	References
Grass carp	*Ctenopharyngodon idellus*	Juvenile	Fresh water	5.26	SBM, RSM,CSM	WO	0.15	Hypoxia-tolerance	Yang et al. (2013)
Grouper	*Epinephelus coioides*	Juvenile	Marine water	13.85	Casein, gelatin	WO	1	Growth, energy utilization, amino acids uptake, protein, lipids and purine synthesis, nutrition metabolism	Shen et al. (2019)
Hybrid snakehead	*Channa argu, Channa maculatus*	Juvenile	Fresh water	28.48	FM, SBM	W	1.5	Survival, resist ammonia stress	Tan et al. (2018)
Japanese flounder	*Paralichthys olivaceus*	Juvenile	Marine water	1.23	FM, casein, gelatin	W	2	Growth, blood parameters, oxidative status	Han et al. (2014)
		Juvenile	Marine water	19.5	BFM, SBM	W	1	Growth, feed efficiency, hematological parameters, immune response	Kim et al. (2017)
Korean rockfish	*Sebastes schlegeli*	Juvenile	Marine water	13.5	wJMM	W	1.5	Growth, feed efficiency, survival, bile acid composition	Kim et al. (2015)
Large yellow croaker	*Larimichthys crocea*	Juvenile	Marine/brackish water	20	WGM, SBM	WO	3.5	Feed efficiency, olfactory-related genes expression	Hu et al. (2018a)
Largemouth bass	*Micropterus salmoides*	Juvenile	Fresh water	19.3	SBM, FM	W	NA	Growth, body composition	Frederick et al. (2016)
Meagre	*Argyrosomus regius*	Juvenile	Marine water	103	SBM, CGM, FM, WM	W	1	Bile acid, lipase activity, cholesterol, Total proteins, Triglycerides	de Moura et al. (2019)
				50	SBM, WM, CGM, FM	W	1	Growth, feed efficiency	de Moura et al. (2018)

Table 1 (continued)

Common name	Scientific name	Life stage	Living environment	Initial BW (g)	Primary protein source(s)	W or WO FM	Tau%	Function(s)	References
Nile tilapia	*Oreochromis niloticus*	Juvenile	Fresh water	6.7	SBM, SPC	WO	0.4	Growth, metabolic response	Michelato et al. (2018)
		Juvenile	Fresh water	4.25	Casein, gelatin	WO	1	Growth, metabolism of amino acids/lipids/energy	Shen et al. (2018)
		Adult	Fresh water	12.5	SBM, FM	W	1	Reproduction performance	Al-Feky et al. (2016a)
		Larvae	Fresh water	0.024	SBM, FM	W	1	Growth, feed efficiency	Al-Feky et al. (2016b)
Parrot fish	*Oplegnathus fasciatus*	Juvenile	Marine water	13.5	FM, casein	W	1	Growth, feed efficiency	Lim et al. (2013)
Persian sturgeon	*Acipenser persicus*	Juvenile	Marine water	26	SBM, WM, WG, FM	W	0.1	Growth, taurine retention	Hoseini et al. (2018)
		Juvenile	Marine water	35	SBM, FM, WG	W	0.25	Growth, feed intake, liver histopathology, carcass moisture and lipids	Hoseini et al. (2017)
Red sea bream	*Pagrus major*	Juvenile	Marine water	108.9	FM, SBM, CGM	W	1	Growth, feed utilization, immunity	Gunathilaka et al. (2019)
				0.5	Casein, gelatin	WO	NA	Cadmium toxicity	Hano et al. (2017)
				0.5	Casein, gelatin	WO	0.5	phenanthrene toxicity	Hano et al. (2016)
				39	FM, SPC	W	1	Epidermal thickness, scale loss	Kato et al. (2014)
Rice field eel	*Monopterus albus*	Juvenile	Fresh water	25.11	FM, SBM, CGM	W	0.15	Growth, lipase activity, total AOC, catalase, lysozyme, T-SOD	Hu et al. (2018b)
Rock bream	*Oplegnathus fasciatus*	Juvenile	Marine water	2.72	FM, WGM	W	0.5	Growth, feed efficiency, protein efficiency	Ferreira et al. (2014)
Sablefish	*Anoplopoma fimbria*	Juvenile	Marine water	50	SPC, CPC, FM	W	1	Growth, FE, nutrient composition	Johnson et al. (2015)
Senegalese sole	*Solea senegalensis*	Juvenile	Marine water	23.7	FM, SMB, FSP, SQM	W	1.5	Lipid digestion, amino acid retention	Richard et al. (2017)
Snapper	*Lutjanus colorado*	Juvenile	Marine water	3.1	FM, SBM	W	1.63	Growth, feed efficiency, body composition	Hernandez et al. (2018)

Table 1 (continued)

Common name	Scientific name	Life stage	Living environment	Initial BW (g)	Primary protein source(s)	W or WO FM	Tau%	Function(s)	References
Tongue sole	*Cynoglossus semilaevis*	Post larvae	Marine water	3.32	FM,KM, SP, casein, SPC	W	1	Growth, enzyme activity, pre-trypsinogen mRNA gene expression	Zheng et al. (2016)
Totoaba	*Totoaba macdonaldi*	Juvenile	Marine water	10	wFM	W	0.45	Growth, green liver, GBSI (gallbladder-somatic Index), ADC (apparent digestibility coefficient)	Satriyo et al. (2017)
		Juvenile	Marine water	7.5	FM, SPC, KM, GELATIN	W	1	Growth, liver histology, hematological and biochemical status	López et al. (2015)
Turbot	*Scophthalmus maximus* L	Juvenile	Marine water	4.16	FM, SBM, WGM, WM	W	0.8	Growth, feed intake, TauT, metabolism	Wei et al. (2018)
				3.66	FM, gluten	W	1.2	Growth, blood glucose level, liver composition, muscle taurine and glycogen	Zhang et al. (2019)
				7.46	FM, CGM, SBM	W	1	Growth, tolerance	Liu et al. (2018)
				3.66	FM	W	1.2	Hyperplasia muscle growth, muscle fiber density, collagen, amino acid, mitochondria, muscle texture	Sampath et al. (2020)
White grouper	*Epinephelus aeneus*	Juvenile	Marine water	19	FM	W	1.5	Growth, lipid metabolism	Koven et al. (2016)
White seabream	*Diplodus sargus*	Juvenile	Marine water	58	SBM, WM, CL, FM	W	1	Growth, feed efficiency	Magalhães et al. (2019)
Yellow catfish	*Pelteobagrus fulvidraco*	Juvenile	Fresh water	5.18	SPC, SBM, CGM, WGM	WO	1.09	Growth, immunity, hyperammonemia	Li et al. (2016)
Yellow drum	*Nibea albiflora*	Larvae	Marine water	0.01	FM, KP, SQM	W	2	Growth, survival	Xie et al. (2014)

Table 1 (continued)

Common name	Scientific name	Life stage	Living environment	Initial BW (g)	Primary protein source(s)	W or WO FM	Tau%	Function(s)	References
Yellowtail	*Seriola quinqueradiata*	Juvenile	Marine water	42	FM, fSBM	W	1.5	Growth, lipid metabolism	Nguyen et al. (2015)
		Adult	Marine water	236	FM, SBM, CGM	W	0.75	Growth, feed efficiency, tissue composition, hematological properties, amino acids in liver and muscle	Khaoian et al. (2014)
Zebrafish	*Danio rerio*	Adult	Fresh water	NA	PP, FM	W	NA	Growth, reproductive performance (not affected)	Guimaraes et al. (2018)

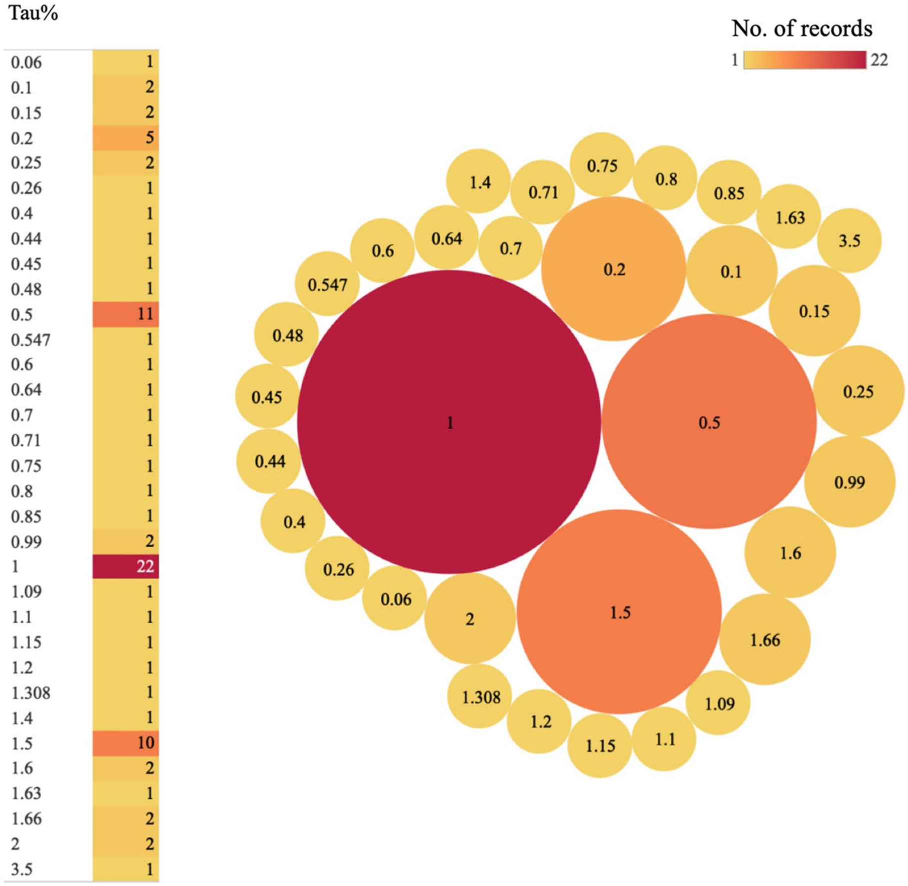
BW body weight, *NA* not available, *W* with, *WO* without, *FM* fishmeal, *Primary protein source(s) FM* fishmeal, *WG* wheat gluten *SPC* soy protein concentrate, *SBM* soybean meal, *CSM* cottonseed meal, *SFM* steamed fishmeal, *WW* whole wheat, *PBM* poultry by-product meal, *SQM* squid meal, *KM* krill meal, *CPC* corn protein concentrates, *CG* corn gluten, *SBMse* SBM solvent extract, *CF* corn flour, *SQP* squid powder, *RSM* rape seed meal, *wJMM* washed jackmackerel meal, *WGM* wheat gluten meal, *WM* wheat meal, *CGM* corn gluten meal; *BFM* brown fishmeal, *SBP* soybean protein concentrates, *wFM* washed fishmeal, *CL* cod liver, *KP* krill powder, *fSBM* fermented SBM, *PP* pea protein

fish. Kim et al. (2017) suggested that dietary taurine content was 0.9–1.3% for Japanese flounder fed with a fishmeal-based diet. Satriyo et al. (2017) suggested that a minimum level of 0.45% of taurine is required in the diet with washed fishmeal as a main protein source to normalize the physiological conditions of juvenile totoaba, namely green liver, low gallbladder-somatic index (GBSI), low plasma total cholesterol, low lipid digestibility, low erythrocyte turnover and low visceral fat content. With most of the cases utilizing more content than the optimal level, dietary taurine has no or negative effects on fish (Hu et al. 2018b; Stuart et al. 2018; Zheng et al. 2016). So, the current knowledge about the optimum dietary taurine levels is highly important for aquaculture as well as for future research. In any case, taurine has shown species specific effects on fish nutrition. So, there were more positive effects as well as a few negative effects on certain fish species. Moreover, taurine is a critical nutrient for plant-based protein diets for fish when considering the growth performance.

Anti-oxidative and immune effects

Taurine has anti-oxidative properties because of its effect on anti-oxidative enzymes and genes in the liver and intestine of fish (Coutinho et al. 2017). According to Zhang et al. (2018), anti-oxidative enzymes, including SOD and GSH-px, in juvenile black carp (*M. piceus*) were significantly increased by dietary taurine supplementation. The interactive effect of dietary taurine and glutamine gave significantly higher anti-oxidative capacity in Japanese flounder (Han et al. 2014). Also, increasing dietary methionine with taurine increased activities of CAT and GPX in the liver of European sea bass (*Dicentrarchus labrax*). Activities of the CAT, T-SOD, and the total anti-oxidative capacity (T-AOC) in rice field eel (*Monopterus albus*) were significantly increased with increasing dietary taurine levels (Hu et al. 2018b). The activities of SOD and the content of glutathione in juvenile black carp (*M. piceus*) were increased by dietary taurine supplementation in low fish meal diet (Zhang et al. 2018). The same results were found in some other species, such as European sea bass (Feidantsis et al. 2014) and common carp (*C. carpio*) (Abdel-Tawwab and Monier 2017).

Juvenile yellow catfish (*Pelteobagrus fulvidraco*) fed with all-plant-based protein diet containing 1.09% of taurine supplementation increased red blood cell, hemoglobin, total immunoglobulin, phagocytic index, respiratory burst and activities of SOD, GPX, CAT and lysozyme in blood (Li et al. 2016). However, when dietary fishmeal was replaced by soy protein concentrates with taurine supplementation, red blood cells, plasmatic hemoglobin and hematocrit in juvenile totoaba (*Totoaba macdonaldi*) were not significantly different from those fed control diet (López et al. 2015). Also, dietary taurine supplementation had no significant



Tau%	
0.06	1
0.1	2
0.15	2
0.2	5
0.25	2
0.26	1
0.4	1
0.44	1
0.45	1
0.48	1
0.5	11
0.547	1
0.6	1
0.64	1
0.7	1
0.71	1
0.75	1
0.8	1
0.85	1
0.99	2
1	22
1.09	1
1.1	1
1.15	1
1.2	1
1.308	1
1.4	1
1.5	10
1.6	2
1.63	1
1.66	2
2	2
3.5	1

Fig. 2 Sum of number of records broken down by recommended/required taurine concentration (%). Circle size and the color show sum of the number of records

effects on immune parameters in white seabream (*D. sargus*) fed with both high and low fish meal diets (Magalhães et al. 2019). The same results were confirmed in Japanese flounder (*P. olivaceus*) (Han et al. 2014). Also, red seabream (*P. major*) fed low fish meal (22–36%) diets in low water temperatures (14.5 ± 1.95 °C) with 1% dietary supplementation had increased innate immunity compared with fish that received high levels of fish meal (45%). However, hematological and biochemical parameters were not affected by taurine supplementation (Gunathilaka et al. 2019).

So, taurine improved the anti-oxidative properties of fish by optimizing the anti-oxidative and immune-related parameters, both at protein and gene levels in the liver and intestine. These parameters include anti-oxidative enzymes (e.g., CAT, SOD and GPX), hemoglobin and total immunoglobulin levels.

Nutrient metabolism

Protein metabolism

Taurine has functional properties in mitochondrial protein synthesis by protecting mitochondria against excessive superoxide generation and enhancing the electron transport chain activity (Chian et al. 2012). Moreover, protein synthesis is a key functional process in nutrition metabolism in fish. TOR regulates the limiting step in protein synthesis. The signaling pathway of the TOR gene expression was significantly increased in the liver of juvenile black carp (*M. piceus*) fed diets with taurine supplementation. However, the TOR gene expression levels in muscle were not significantly affected by dietary taurine (Zhang et al. 2018).

Dietary taurine significantly increased the protease content in common carp (*C. carpio*) (Abdel-Tawwab and Monier 2017). The protein efficiency ratio was significantly improved by 1.2% of dietary taurine, and the whole-body protein content was not affected in juvenile European sea bass (*Dicentrarchus labrax*) (Martins et al. 2018). However, the whole-body protein content in cobia (*Rachycentron canadum*) was increased with dietary taurine content (Watson et al. 2013). Also, grouper (*Epinephelus coioides*) fed dietary taurine improved amino acid uptake and protein synthesis by the actions of metabolic regulation in the protein synthesis pathway (Shen et al. 2019). So, taurine has improved the protein metabolism in fish by optimizing the mitochondrial protein synthesis and TOR gene expression.

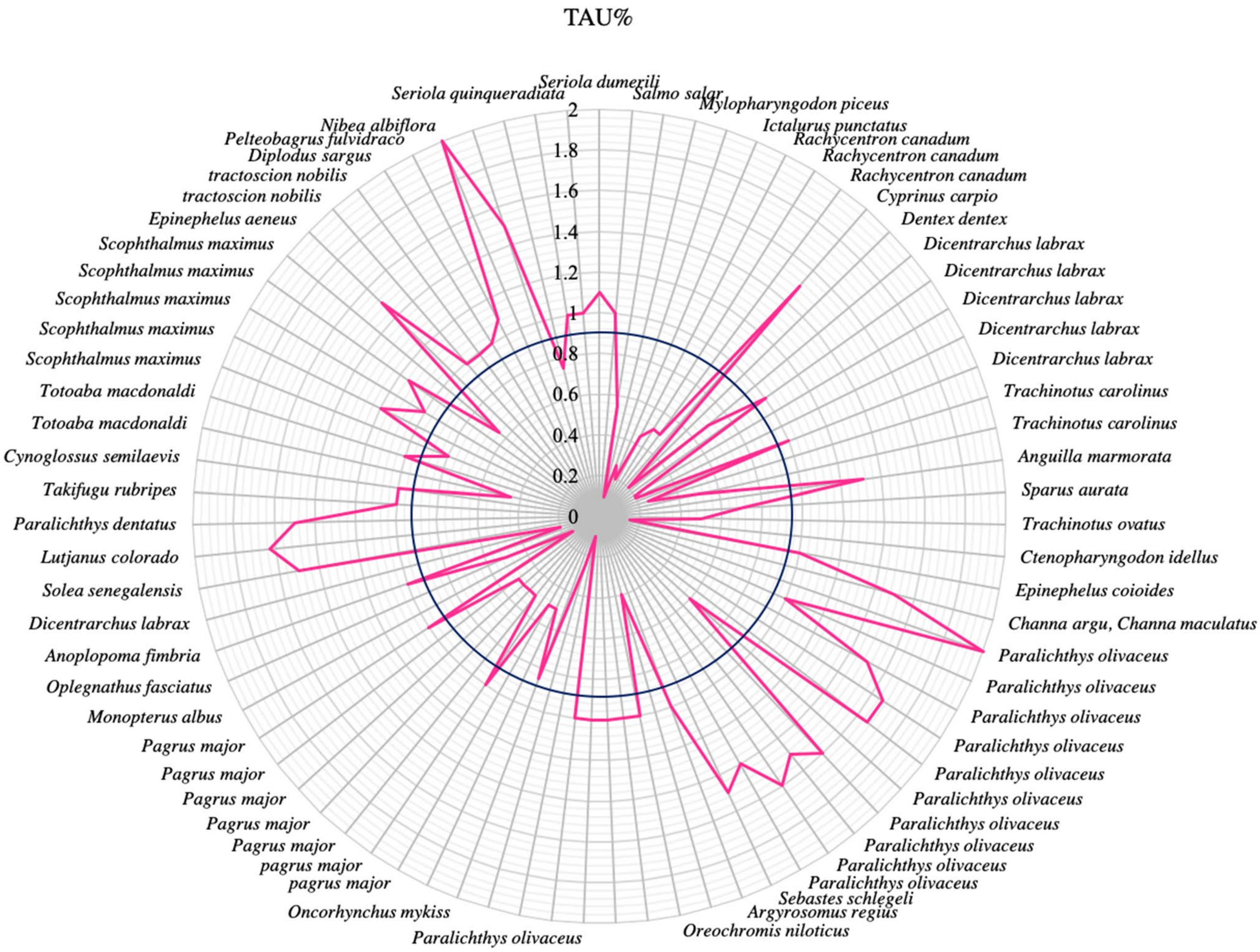


Fig. 3 Radar plot of tested taurine-supplemented percentage with fish species and their life stages. Highlighted circle is the mean value of taurine% (0.91)

Glucose metabolism

The efficiency of carbohydrate metabolism in fish mainly depends on the enzyme activity, insulin receptors, rate of glucose transport and regulation efficiency of hepatic glucose utilization. Dietary taurine supplementation increased the activity of intestinal amylase in turbot (Zhang et al. 2019), common carp (Abdel-Tawwab and Monier 2017) and black carp (*M. piceus*) (Zhang et al. 2018). Synergic effects of dietary taurine and carbohydrates significantly decreased the gene expression of fructose-1, 6-bisphosphate and glycation end products in the plasma of turbot (*Scophthalmus maximus*) (Zhang et al. 2019). The gene expressions of liver glucokinase, phosphofructokinase, pyruvate kinase, glucose-6-phosphate dehydrogenase (G6PD), glycogen synthase (GS) and glucose transporter 2 were significantly increased. Conversely, liver cytosolic phosphoenolpyruvate carboxykinase (cPEPCK) expression in turbot was significantly decreased with 1.2% of dietary taurine supplementation (Zhang et al. 2019). Dietary taurine increased glucose phosphorylation and the activity of hepatic G6PD in totoaba (*T. macdonaldi*) fed soy protein concentrate-based diet. Meanwhile, it decreased the catabolic enzyme activity of glucogenesis (Bañuelos-Vargas et al. 2014). Taurine has blood glucose reducing properties via interaction with the insulin receptors. It was found that dietary taurine supplementation decreased the plasma glucose levels in white seabream (*D. sargus*) (Magalhães et al. 2019). Moreover, dietary taurine supplementation increased the glucose tolerance ability of turbot (Zhang et al. 2019).

In a word, taurine improved the glucose metabolism by enhancing the activities and gene expression of enzymes, such as glucokinase, phosphofructokinase, pyruvate kinase, glucose-6-phosphate dehydrogenase, glycogen synthase and glucose transporter 2.

Lipid metabolism

Bile acid has key roles in lipid metabolism. Taurine has a direct correlation with bile acid metabolism in fish liver. Bile salts are synthesized in liver as a derivative of cholesterol. Bile acids are secreted into the intestine to emulsify lipids, to increase the fat-soluble vitamin absorption and enhance dietary lipids (Magalhães et al. 2019). Soybean meal (SBM) is the main fishmeal replacement in most plant-based fish feed formulae. However, lack of taurine in SBM diets resulted in abnormalities of lipid digestion. Yellowtail (*S. quinqueradiata*) fed an SBM-based diet with 0.15% of taurine content had significantly lower lipid digestibility than those fed a fishmeal-based diet with 0.24% of taurine content. At the same time, lipase activity in the anterior intestine, the lipid content in liver and muscle, and bile acid concentrations in the gall bladder and interior intestinal track were significantly lower in the SBM group than in the FM group. The lipid digestion of yellowtail was significantly increased by the fishmeal-based diet than the SBM-based diet without dietary taurine supplementation. These results suggested that taurine has significant effects on lipid metabolism, lipid digestion and the lipid absorption in fish. Taurine supplementation in SBM-based diet restored lipid digestibility, bile acid concentration and tissue lipid concentration of yellowtail (Nguyen et al. 2015). Triglyceride and cholesterol levels in juvenile yellow catfish (*Pelteobagrus fulvidraco*) fed all-plant protein diets were significantly decreased with the increasing dietary taurine levels up to 2.55% (Li et al. 2016). Also, meagre (*A. regius*) fed high plant protein diets with 1% taurine had significantly increased total bile acids in the plasma as well as the anterior intestine, total plasma cholesterol and triglycerides (Moura et al. 2019). Dietary taurine significantly reduced the liver lipid peroxidation in totoaba (*Totoaba macdonaldi*) (Bañuelos-Vargas et al. 2014) and zebrafish (*D. rerio*) (Rosemberg et al. 2010). The whole-body lipid content in juvenile black carp (*M. piceus*) fed dietary taurine was significantly decreased (Zhang et al. 2018). In addition, lipase activity in the intestine of juvenile black carp (*M. piceus*) and turbot (*Scophthalmus maximus*) was significantly increased with taurine supplementation in low fish meal diet (Zhang et al. 2018, 2019). Meanwhile, dietary taurine increased the lipid metabolism of grouper (*Epinephelus coioides*) by optimizing the lipid digestion and metabolic regulation (Shen et al. 2019). Thus, taurine has important roles in lipid metabolism in fish, including bile acid synthesis, lipid emulsification, lipid digestion and absorption, and body lipid deposition.

Reproductive and larval performances

Most of the published studies focus on juvenile fish, there are fewer data dealing with the broodstock and larvae. Taurine was determined as an essential nutrient in broodstock diets. For example, greater amberjack (*Seriola dumerili*) has multiple spawning patterns. Dietary taurine increased the fertilization rate, fecundity, egg diameter, egg protein content, larger yolk sac volume and larval quality (Sarih et al. 2019). Yellowtail broodstock fed with dietary taurine had increased oocyte growth, spawning success and reduced egg abnormalities (Matsunari et al. 2006). Also, Nile tilapia broodstock had significantly higher spawning frequencies, total spawning, hatchability, number of spawnings per female and absolute fecundity with increasing dietary taurine content up to 1%. It was suggested that 0.8% of dietary taurine is required for optimum reproductive outputs of Nile tilapia broodstock (Al-Feky et al. 2016a). However, zebrafish fed with graded levels of dietary taurine from 0.02 to 1.37% were not significantly affected for reproduction with plant protein-based diet. Yet, it was recommended to have taurine in the broodstock diet of zebrafish to improve lipid utilization and redox status (Guimaraes et al. 2018).

Abdel-Tawwab and Monier (2018) pointed out that 1.5% of dietary taurine significantly increased the growth, feed intake and activities of the intestinal amylase, lipase and protease of common carp larvae. Gilthead seabream larvae fed dietary vitamin E and C with taurine had significantly increased gene expression of osteocalcin (OC), but not catalase (CAT), glutathione peroxidase (GPX) and superoxide dismutase (SOD) (Izquierdo et al. 2019). However, dietary taurine significantly affected the anti-oxidative capacity of common carp larvae by increasing the activities of SOD, CAT and GPX. Regarding gilthead seabream, 0.71% of dietary taurine significantly increased the growth of larvae (Izquierdo et al. 2019). Up to 1% of dietary taurine significantly increased the growth and feed utilization of Nile tilapia larvae fed with the soybean meal-based diet. Meanwhile, body protein and body amino acid contents were significantly increased, whereas body moisture and ash levels were decreased. However, body lipid contents were not significantly affected by dietary taurine (Al-Feky et al. 2016b). Also, it was found that taurine significantly increased the survival, growth performance and taurine content in the body of yellow drum *Nibea albiflora* larvae (Xie et al. 2014). Taurine has antioxidant properties with a combination of vitamin C and E in the larval diet. It significantly increased the growth of gilthead seabream larva fed with 0.71% of dietary taurine. Meanwhile, it reduced bone anomalies through up-regulating the osteocalcin gene expression, and down-regulating the anti-oxidative enzyme genes (Izquierdo et al. 2019). Taurine is a limiting nutrient in the feed for California yellowtail (*Seriola lalandi*) larvae. However, dietary taurine supplementation had no significant effects on white seabass (*Atractoscion nobilis*) larvae (Rotman et al. 2017). Tongue sole (*Cynoglossus semilaevis*) postlarvae fed with dietary taurine had significantly increased survival, growth, trypsin activity and gene expression of pretrypsinogen (Ptry). Excessive dietary taurine (2%) had negative effects on survival, growth and the enzyme activities (Zheng et al. 2016). However, even 12.2% of dietary taurine had no significant negative effects on the growth, survival and feed consumption rates of California yellowtail (*Seriola dorsalis*) postlarvae (Stuart et al. 2018). Certainly, more research is needed to evaluate the potential nutrient toxicity of elevated dietary taurine concentrations for fish larvae.

Taurine transporter (*TauT*) gene expression

TauT is the key gene to transport taurine from intercellular plasma to cell plasma as well as cell plasma to mitochondria (Schuller-Levis and Park 2003). Intracellular taurine accumulation is mainly controlled by *TauT*, which contributes to taurine transportation in cells and the mitochondria in fish. *Tau* facilitates taurine synthesis in the liver by increasing the efficient transportation system in the cells. According to Schuller-Levis and Park (2003) and Liu et al. (2017), *TauT* contributes to mitochondrial taurine biosynthesis and membrane taurine transportation (Fig. 4). According to the NCBI nucleotide database, *TauT* gene sequences have more similarities between fish species (Fig. 5). It has been shown that there are similar sequences between fish species. So, taurine has optimized taurine transportation at the cellular level by affecting *TauT* gene expression.

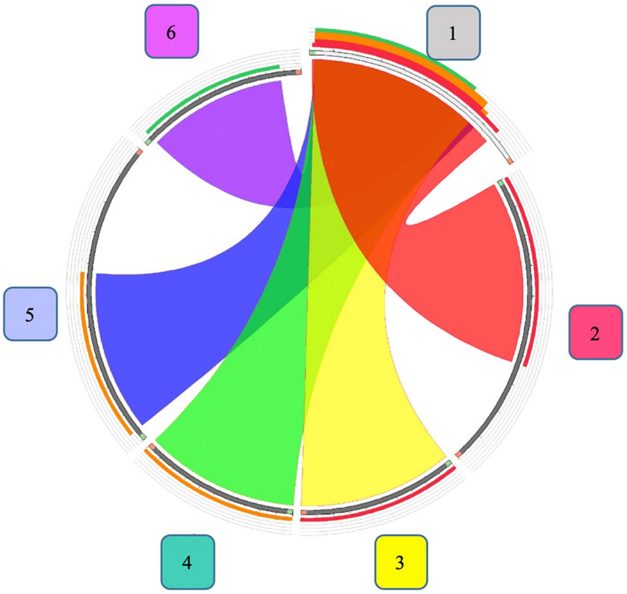


Fig. 5 Circos plot of TauT mRNA sequences similarities between different fish species with NCBI GenBank accession no. (1). *Scophthalmus maximus*: KT369001.1, (2) *Oreochromis mossambicus*: AB033497.1, (3) *Solea senegalensis*: HQ148721.1, (4) *Siniperca chuatsi*: KP689601.1, (5) *Lateolabrax japonicas*: JN897395.1, (6) *Epinephelus coioides*: KX226453.1

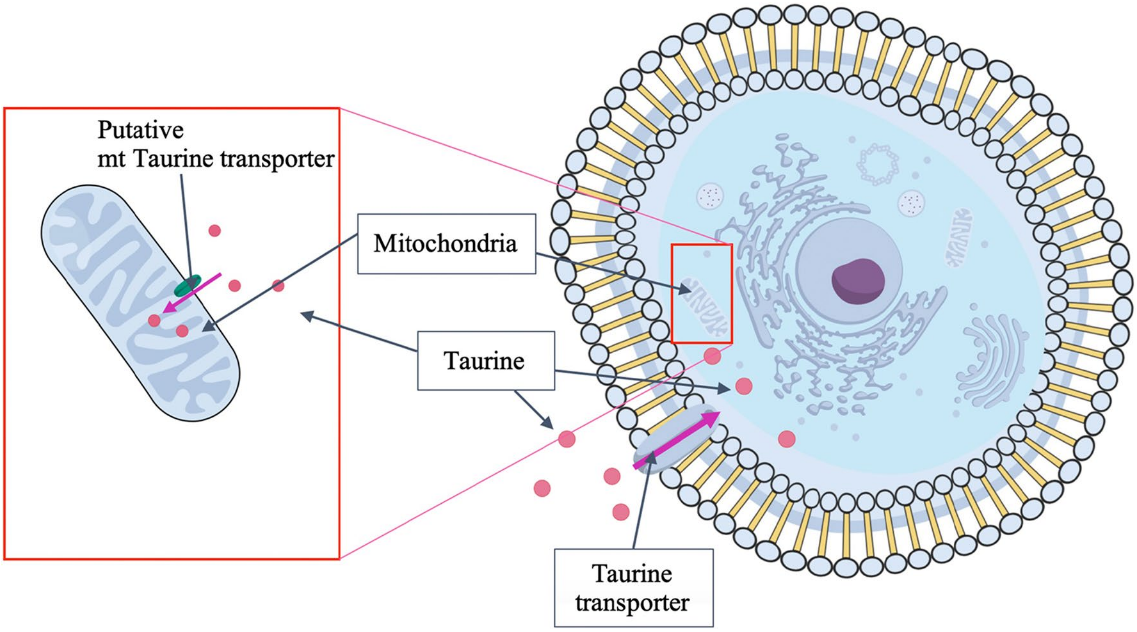


Fig. 4 Mitochondrial taurine transportation biological pathway

Concluding remarks

A large number of publications suggest that fish growth is significantly increased, i.e., between 0.5 and 1.5%, with dietary taurine supplementation. The optimum growth performance may be obtained with dietary taurine supplementation in the juvenile stage due to high growth-related metabolic functions. In addition, taurine increases the egg fertility of the brood stock and the survival rate of larvae. Dietary taurine supplementation mainly affected growth performance, feed efficiency, muscle texture and composition, feeding behavior, metabolic functions (protein, lipids and carbohydrate), anti-oxidative capacity and immunity of fish. Moreover, plant based diets are recommended with taurine supplementation because of the lack of this compound in plant protein. However, taurine effects are species specific and dose dependent. Even in the same fish species, growth parameters are different according to the environmental conditions, broodstock health, immunity and the presence of other nutrient combination in the fish diets. Further studies are highly recommended to identify the effects of taurine on different fish species, and their different life stages, especially the juvenile stage.

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Author contributions WWHAS: methodology, data collection, analysis and manuscript writing; RMDSR: data collection and analysis; MY: data collection and filtering; WZ: funding acquisition, supervision, Writing—review and editing; KM: supervision.

Compliance with ethical standards

Conflict of interest The authors have declared that no conflict of interest exists.

Animal and human rights statement The present study did not violate any animal or human rights.

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