



## Dietary Taurine Supplementation Influence on the Growth and Metabolicactivity of Fish: Juvenile, Cichlid, and Teleost

Syeda Rida Zahra Naqvi<sup>1\*</sup>, Zai-Zhong Chen<sup>1</sup>, Ruqia Bibi<sup>2</sup>, Tooba Zainab<sup>3</sup>,  
Tabinda Laraib<sup>4</sup>

<sup>1</sup>College of Fisheries and Life Science, Shanghai Ocean University, 201306 Shanghai, China; the National Demonstration Center for Experimental Fisheries Science Education, Shanghai Ocean University, Shanghai 201306, China

<sup>2</sup>Department of Zoology, Ghazi University, Dera Ghazi Khan , Pakistan

<sup>3</sup>Department of Zoology, University of Sargodha, Sargodha, Pakistan

<sup>4</sup>Institute of Forest Science, the Islamia University of Bahawalpur, Bahawalpur, Pakistan

\*Corresponding Author: syedaridazahra8672@gmail.com

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### ABSTRACT

Taurine (2-aminoethane sulfonic acid) is  $\beta$ -amino acid based exclusively on plant protein. Moreover, it is a small organic compound that contains sulphur and is present in a large amount in various organs, such as the liver, retina, kidney, and the intracellular space of the brain, blood cells, muscles, tissues, and the heart of the invertebrate species. Taurine contains two functional groups, one is an alkaline amino group, while the other is an acidic sulfonic group. Review articles have demonstrated the beneficial impact of dietary taurine on the growth and metabolism of various fish species upon using as a dietary supplement. The role of taurine for underlying metabolic functions have been poorly understood. After reviewing the literature, some changes in metabolic functions were described, including the alterations in the content of the amino acids, nucleotides, lipids, and carbohydrates. The results showed that the growth and physiological functions in the body of fish may greatly be regulated by dietary taurine supplementation in fish species. The activity of cysteine sulphinate decarboxylase (CSD) plays an important role during taurine biosynthesis. This study recapitulated the existing information on the functions of dietary taurine in fish, principally in the juvenile, the cichlid fish (The Nile tilapia), and the teleost. In addition, this review emphasized the structure of taurine, its physiological functions, biosynthesis, and the effects of dietary taurine on fish growth, health, and metabolic functions when included as a supplement in their diet..

### INTRODUCTION

Taurine is found in the tissues of animals mostly in plasma, muscles, heart, and leucocytes. It acts as an antioxidant and exist in a trace amount. Taurine is not used for the synthesis of protein; however, it plays a major role in detoxification, stabilization of membrane, transport of calcium, development of retina, neurotransmitter modulation, endocrine functions, osmotic regulation, metabolism of methionine, transport of inner

membrane, metabolism of sulfur and biosynthesis, as well as in the metabolism of bile salt (Salze & Davis, 2015). In the history, taurine has been deliberated as a non-essential nutrient for fish diet. However, current investigation demonstrated that dietary taurine can be synthesized by the transulfuration process in fish (Salze & Davis, 2015). Taurine is synthesized from methionine. In plants, a limiting amino acid plays a vital role in the production of taurine and cysteine (Jobling, 2012). The biosynthesis of taurine is critically different in various fish species. Moreover, a rich amount of taurine is present in fish meal (Salze & Davis, 2015). A better quality and larger percentage of dietary taurine is essential for the growth of fish than land animals. In aqua feeds, fish meal acts as a major source of protein for the omnivorous and carnivorous fish (Michelato *et al.*, 2018). Several studies have demonstrated that a deficiency in taurine can result in disturbances and abnormalities in physiological functions, growth, and metabolism. Therefore, taurine is an essential dietary component for promoting growth in many marine and freshwater fish species, such as the white grouper (*Epinephelus aeneus*), the Nile tilapia (*Oreochromis niloticus*), and the yellow catfish (*Pelteobagrus fulvidraco*) (Li *et al.* 2016; Shen *et al.* 2018). The necessity of taurine is depending upon some factors like the natural feeding history of fish and the feeding habit of fish species (Li *et al.*, 2016). Moreover, according to Salze and Davis, “some cultured fish in their diet contain the optimal requirement of dietary taurine that ranges from 0.20 to 1.66%” (Salze & Davis, 2015). Though, recent studies primarily focused on the effect of dietary taurine supplementation on the growth performance in fish, while the role of taurine for underlying metabolic functions have been poorly understood yet. In recent times, numerous studies have showed that in the pathway of the biosynthesis of dietary taurine, there are some interspecific differences in the fish body (Goto *et al.*, 2003). Synthesis of taurine via sulfate instead of cysteine might result in insufficient amount, affecting the growth of fish (Martin *et al.*, 1966). The taurine content in the eyes and brain (central nervous system) depends on the level of taurine in the fish diet. Additionally, the osmotic regulation of taurine may play a significant role in the central nervous system. In many tissues of the marine fish, taurine contains greater than 50% of the free amino acid pool (Lombardini *et al.*, 1979). Sometimes, aquatic animals consume other species in the marine environment that contain higher quantities of taurine. This can cause a decline in plasma osmolarity, necessitating the evacuation of excess taurine. Renal tubular secretion of taurine occurs in fish, resulting in its excretion through urine (King *et al.*, 1982). According to Chesney *et al.* (1998), taurine is an important osmolyte in the renal medulla and brain of infants. Its medical significance is evident, as the taurine depletion in infants may affect their response to hyponatremic or hypernatremic stress and cause significant variations in neuronal volume. The high level of intracellular taurine is maintained by a sodium-dependent taurine transporter in the plasma membrane.

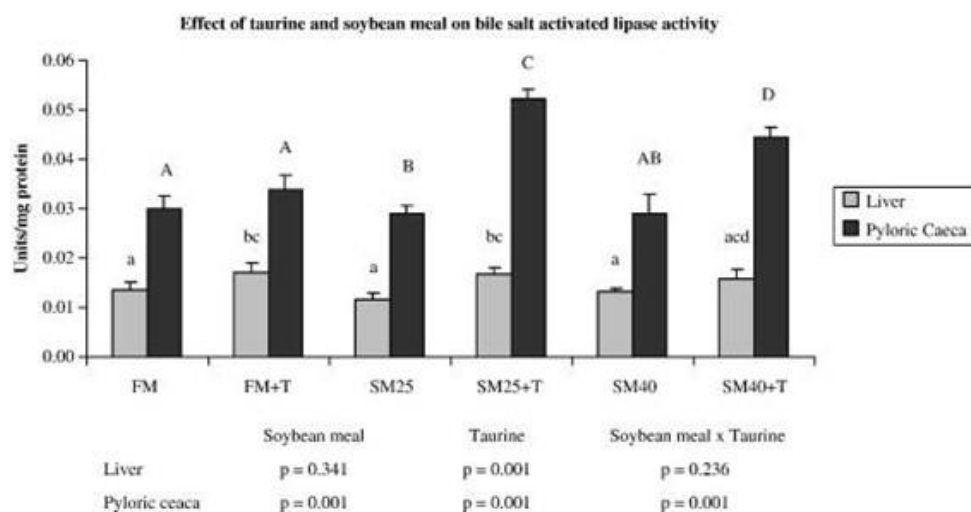
Additionally, the dietary taurine content in the muscle of rainbow trout (**Yokoyama & Nakazoe, 1992**) and other fish fed taurine-supplemented diets remained consistent, regardless of dietary taurine levels. Conversely, Park and colleagues observed that taurine content in the muscle of the juvenile yellowtail and the whole body of the juvenile Japanese flounder increased with higher levels of dietary taurine (**Park et al., 2002**). Thus, the marine fish rely on dietary taurine to maintain their body taurine pool. The required amount of dietary taurine for the juvenile marine fish, such as the European sea bass, yellowtail, and the Japanese flounder is 0.2%, greater than 1.0%, and 1.5- 2.0%, respectively. Researchers found that dietary taurine supplementation made the diet of the parrot fish more palatable (**Lim et al., 2013**).

When methionine-supplemented fish meal was fed to the rainbow trout, there was an increase in the cystathionine content in the liver and a decrease in the serine content (**Yokoyama & Nakazoe, 1992**). In the rainbow trout, dietary taurine levels in plasma and liver increased with higher cystine levels in the diet, and the content of the hypotaurine in the kidney and liver also increased significantly with higher cystine levels (**Yokoyama & Nakazoe, 1998**). On the other hand, the juvenile flounder showed increased levels of taurine in the body, muscle, and liver with dietary taurine supplementation, as they lack the ability to biosynthesize taurine from the dietary cystine (**Park et al., 2002**).

Marine species can develop a pathological condition known as green liver due to bile pigment accumulation. Studies indicated that large amounts of soybean in the fish meal caused green liver in the yearling red sea bream, which was prevented by dietary taurine supplementation. However, the necessity of dietary taurine in the red sea bream has not been determined across the juvenile, young, or adult stages (**Takagi et al., 2006a**). Dietary taurine is involved in sulfur amino acid metabolism of the juvenile Japanese flounder (*Paralichthys olivaceus*) and enhances their feed intake (**Park et al., 2002**). The presence of dietary taurine in fish meal and its significance for numerous species have been proven.

It has been demonstrated that the growth of the turbot larvae was significantly associated with the dietary taurine (**Conceição et al., 1997**). Dietary taurine is crucial for the proper growth and feeding behavior of the Japanese flounder (**Takeuchi et al., 2001**). The Japanese flounder fed on dietary taurine exhibited an improved settlement at the bottom of the tank and feeding behavior similar to the wild fish, unlike those in the low taurine-fed groups (**Takeuchi et al., 2001**). For better immunity, disease resistance, and growth of the juvenile yellow catfish (*Pelteobagrus fulvidraco*), a dietary taurine supplementation of 1.09% was needed (**Li et al., 2016**). The estimated optimal dietary taurine amount for the juvenile Japanese flounder is 1.4% (**Park et al., 2002**).

Taurine plays an important role in the formation of bile salts (Vessey *et al.*, 1990) by stimulating the activity of the enzyme cholesterol 7 $\alpha$ -hydroxylase during the biosynthetic process (Anitha Nandhini *et al.*, 2002). Moreover, the salt-activated lipase becomes active in the presence of the bile salt (Lombardo *et al.*, 1980). The activity of the bile salt-activated lipase in the liver depends on the presence of the bile salt, not on the fish meal replacement level by soy protein essence. However, the activity increased in fish fed three diets: soybean meal 25 (SM25), fishmeal (FM), and soybean meal 40 (SM40) with added taurine ( $P < 0.05$ ). Similarly, soy protein and dietary taurine essence in the pyloric caeca increased the enzyme activity in the liver when soy protein essence was present in the diet, indicating that this rise depends on its presence (Chatzifotis *et al.*, 2008).



**Fig. 1.** Activity of bile salt-activated lipase (Units/mg protein) in the pyloric caeca and liver of common dentex, *Dentex dentex*, fed different meals. Values with the same letters do not differ significantly ( $P < 0.05$ ) (Chatzifotis *et al.* 2008)

Dietary taurine enhances the feed intake and growth rate of the common dentex. In the rainbow trout, the concentration of taurine in plasma decreases a few hours after feeding on a taurine-supplemented meal. This decrease is likely due to the bile acid conjugation with dietary taurine for lipid digestion (Yamamoto *et al.*, 2005). The nutritional importance of plant protein diets is increased by dietary taurine, which also improves their palatability.

Several studies show that dietary taurine has significant stimulatory effects on the olfactory organs of various the fish species, such as the rainbow trout (Hara *et al.*, 1984), grayling, and the Arctic charr (DØVING *et al.*, 1980). Additionally, behavioral studies have predicted that low concentrations of dietary taurine (10 to 12M) attract the European

glass eels (**Sola & Tosi, 1993**). It was reported that dietary taurine stimulates chemoreceptor cells and enhances the taste for the American lobster and exerts feeding stimuli for the tiger prawn (*Penaeus monodon*) (**Borroni et al., 1986**).

It is suggested that, similar to other animal species, taurine may affect the lipid metabolism in fish species, where hypolipidemic effects are exhibited by taurine (**Militante & Lombardini, 2004**). The hypolipidemic effect of dietary taurine is associated with accelerating the synthesis of the bile acid (**Shen et al., 2018**) and subsequently activating bile salt-activated lipase. However, there was no beneficial effect of taurine on the juvenile and fingerling rainbow trout when fed a methionine hydroxyl analogue (MHA) supplemented diet (**Yokoyama & Nakazoe, 1992**).

It is clear that taurine is a conditionally essential amino acid. Additionally, when the juvenile rainbow trout were fed a soy protein essence diet containing MHA, they presented high levels of plasma taurine, likely due to the transformation of dietary MHA into dietary taurine, which prominently promoted the fish growth (**Boonyoung et al., 2013**).

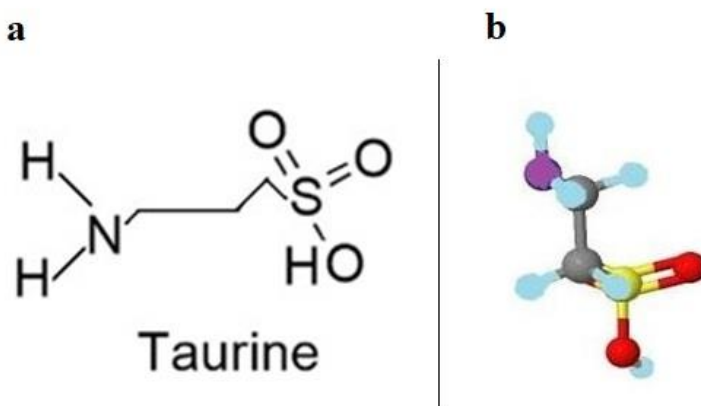
This review will emphasize the structure and functions of dietary taurine in fish by deliberating various studies available. It will principally focus on the juvenile, cichlid fish (The Nile tilapia), and the teleost species, discussing how dietary taurine affects growth, feeding ability, and metabolism in different fish species. It is hoped that this discussion will expand our knowledge about the functions of dietary taurine in aquaculture.

### **Chemical structure of taurine**

During the metabolism of sulfur-containing amino acids, an end product known as taurine is formed. The International Union of Pure and Applied Chemistry (IUPAC) name for taurine is 2-aminoethanesulfonic acid, and its chemical formula is  $C_2H_7NO_3S$ . Taurine is a neutral  $\beta$ -amino acid with both sulfonic and amine groups that can be ionized (**Jacobsen & Smith, 1968**). Notably, taurine is neither degraded by mammalian tissues nor assimilated into proteins (**Kuzmina et al., 2010**). However, taurine accounts for 30 to 50% of the total amino acid pool, making it a highly abundant free amino acid in animal tissues, depending on the species (**Jacobsen & Smith, 1968**).

Taurine is primarily found in various animal tissues, including muscles, retina, heart, brain, blood cells, and the large intestine (**Schuller-Levis & Park, 2003**).

Fig. (2a) below shows the two-dimensional chemical structure of taurine, also known as the skeletal formula. This is a standard notation for organic molecules, where carbon atoms are implicitly represented at the corners, and hydrogen atoms attached to carbon are not shown. Each carbon atom can form four bonds with hydrogen. Fig. (2b) displays the three-dimensional chemical structure of taurine, using a ball-and-stick model. This model illustrates the bonds between atoms and their three-dimensional positions, with the rods representing bonds being longer than the radius of the spheres representing atoms. This provides a clear visual representation of both the bonds and atoms in taurine's chemical structure.



**Fig. 2.** (a) Two-dimensional chemical structure of taurine. (b) 3-dimensional chemical structure of taurine

### Name and nature of taurine

The origin of taurine's name dates back to its first isolation from the bile of the ox, *Bos taurus* (**Demarçay, 1838**). Taurine exhibits high water solubility and low lipophilicity, attributing to its zwitterionic nature (**Jacobsen & Smith, 1968**).

### Dietary sources of taurine

Dietary taurine is primarily abundant in animal protein sources, including eggs, seafood such as fish, crabs, oysters, clams, mussels, and shrimp, as well as in milk and dairy products in addition to meat (**Jacobsen & Smith, 1968**). Marine algae also contain varying levels of taurine. However, taurine is typically lacking in higher plant tissues like soybean. Table (1) summarizes some common food sources containing taurine content.

### Distribution of taurine in fish

Various studies have highlighted the distribution of taurine across different species. Generally, animals across the kingdom, except protozoans, tend to have higher

concentrations of taurine compared to other kingdoms, where it is relatively low or absent altogether. Species with cells lacking rigid cell walls typically have higher taurine concentrations, while those with rigid cell walls tend to have lower or absent taurine concentrations. Some fish species lack the ability to biosynthesize taurine in their bodies and therefore require dietary supplementation (**El-Sayed, 2013**). Taurine is commonly found in fish species, particularly in marine animals. Remarkably high concentrations of taurine have been reported in certain fish tissues. For instance, the dark muscle of the yellowtail or Japanese amberjack (*Seriola quinqueradiata*) contains approximately 83 micro moles/ gram wet weight, while the tilapia contains a more modest with 9.1 micro moles/ gram. In the heart of the rainbow trout (*Oncorhynchus mykiss*), the concentration is approximately 48.7 micro moles/ gram, and in the gills, it's about 35.2 micro moles/ gram compared to 0.73 micro moles/ gram in the plasma (**Gras et al., 1982**). However, it should be noted that these values likely depend on the wet weight.

### **Dietary taurine biosynthesis**

The biosynthetic pathways of taurine have been a focal point of research for several decades although some aspects remain poorly understood (**Jacobsen & Smith, 1968**). In mammals, the primary pathway for taurine synthesis from cysteine involves the oxygenation of cysteine into cysteine sulfinic acid, followed by decarboxylation into hypotaurine, which is then converted into taurine (**Worden & Stipanuk, 1985**). However, it has been noted in many studies that the process of taurine synthesis varies among fish species and may be influenced by different developmental stages in fish (**Kim et al., 2005**). This variation is perhaps due to the unpredictable activity of the main enzyme L-cysteine sulfinic acid decarboxylase, which is crucial for the conversion of cysteine into taurine (**Takeuchi et al., 2001**). Pathways from cysteine to taurine have been observed in the Japanese flounder and rainbow trout (**Yokoyama & Nakazoe, 1998**). The juvenile flounder, for example, lacks the ability to utilize cysteine for the biosynthesis of taurine. However, the supplementation of taurine in the diet of the juvenile flounder can elevate the levels of taurine in the liver, muscle, or entire body of the fish (**Park et al., 2002**).

In some studies, it has been demonstrated that the supplementation of cysteine into a casein-based semi-purified diet did not increase the taurine content or promote growth in the juvenile red sea bream. The activity of the enzyme cysteine sulfinic acid decarboxylase (CSD) in the red sea bream is approximately half of that observed in the rainbow trout. This enzyme plays a role in the trans-sulfuration pathway from cysteine sulfinic acid to hypotaurine. Therefore, the capacity for taurine biosynthesis from cysteine may be low in the juvenile red sea bream. Amino acids containing sulfur undergo essential catabolic processes to synthesize taurine (**Kuzmina et al., 2010**).

**Table 1.** Concentrations of taurine in different foodstuffs (mg kg<sup>-1</sup> wet weight) (Rana & Sanders, 1986)

Source	Concentration of taurine (mg kg <sup>-1</sup> )	Source	Concentration of taurine (mg kg <sup>-1</sup> )
<b>Seafood</b>		Chicken/raw dark meat	1690*
Squid	3560†	Turkey/raw dark meat	3060*
White fish/raw	1510*	Ham/baked	500*
Farmed salmon	600‡	Beef/raw	43*, 430†
Cod/frozen	310*	<b>Milk and derivatives</b>	
Plaice	1460‡	Ice cream vanilla	19*
Scallop	8270†	Cow's milk, Homogenized	151†
Tuna red meat	2798†	Yogurt/low fat plain	33*
Mackerel	780‡	<b>Feedstuffs</b>	
Wild salmon	600‡	Whey	1004†
Greenland halibut	320‡	Poultry by-product Meal	3049†
Tuna/canned	420*	Tuna meal	1060†
Cod	1080‡	Fish protein hydrolysate	7501†
Albacore tuna	1760‡	Meat and bone meal	956†
Oysters/fresh	700*, 3960†	Salmon meal	3106†
Clams/fresh	2400*	Fishmeal	3201†
Tuna/whole	2840†	Rhodophyta ( <i>Grateloupia elliptica</i> )	24.8†
Clams/canned	1520*	Rhodophyta (Gelidium subcostatum)	1094†
Mussels/raw	6550*	Yeast	112†
<b>Meat</b>		Fish scrap	1083†
Pork/raw	610*	Chicken viscera	1004†
Chicken leg	337†	Meat meal	1150†
Lamb/raw dark meat	470*	Shrimp meal	1094†
Beef carcass	296†	Phaeophyta ( <i>Laminaria japonica</i> )	112†
Turkey	932†		

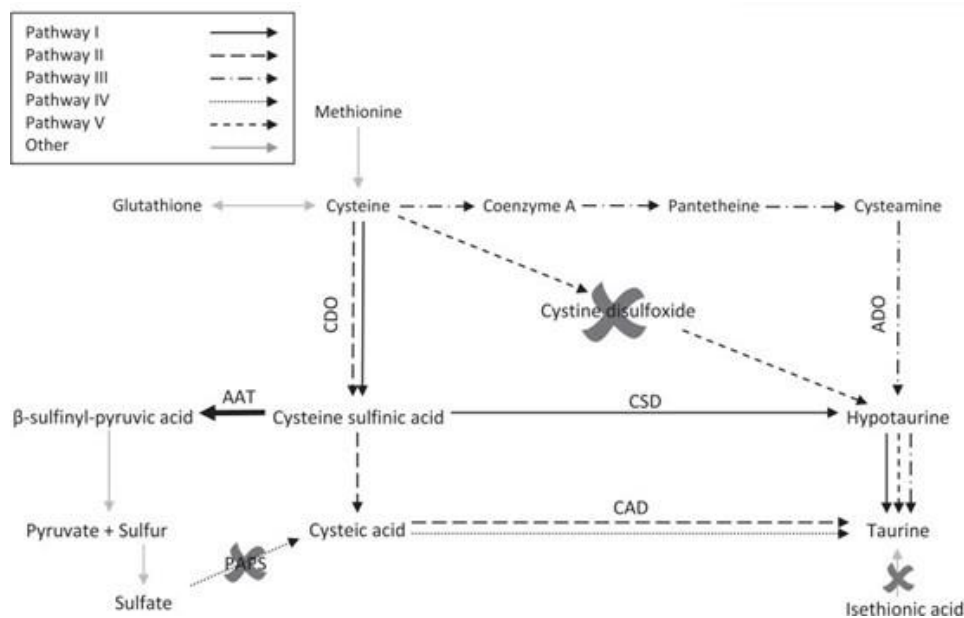
(Lourenco & Camilo, 2002; Spitze *et al.*, 2003; Gormley *et al.*, 2006).

The primary route for taurine biosynthesis depends on tissue types and varies between species. Due to limited activity of CSD, some species lack the ability to synthesize this amino acid. In several mammalian species, the endogenous synthesis of taurine mainly occurs in the brain and liver through the conversion of methionine into cysteine or enzymatic oxidation and direct conversion of cysteine (Jacobsen & Smith, 1968). In rats, the taurine pathway in the liver causes 70% degradation of cysteine to



pyruvate or taurine. Cysteine dioxygenase (CDO) activity leads to cysteine sulfinic acid, followed by cysteine sulfinic acid decarboxylase. Vitamin B6, also known as pyridoxine, is required for the conversion of methionine or cysteine to taurine.

Historically, taurine has been considered a non-essential nutrient in the fish diets (Brosnan & Brosnan, 2006). However, recent research indicates that different fish species have varying mechanisms for taurine synthesis, depending on factors such as feeding habits, size, species, and CSD activity. Some marine species, viz. the red sea bream, Japanese flounder, and the yellowtail, have limited or negligible ability for taurine synthesis, especially at the juvenile stage. In contrast, the freshwater teleost fish, such as the Atlantic salmon, rainbow trout, and common carp, utilize the trans-sulfuration pathway with the assistance of aspartate aminotransferase (AAT) for taurine synthesis. Tissue taurine concentration in these freshwater fish increases with dietary methionine and cysteine supplementation. Even bluegill have the capability for taurine synthesis, albeit with lower cysteine sulfinic acid decarboxylase activity in individuals fed with diets containing deficient taurine concentrations. It has been suggested that feeding history and natural feeding habits of fish can affect taurine synthesis through their influence on cysteine sulfinic acid decarboxylase activity (Gaylord *et al.*, 2006). This discussion sheds light on the varying ability of the herbivorous fish like the tilapia and grass carp, as well as the carnivorous fish such as the rainbow trout, Atlantic salmon, and channel catfish, to synthesize taurine from methionine or cysteine. Recent studies have described five pathways for the biosynthesis of taurine (Jacobsen & Smith, 1968).



**Fig. 3.** Pathways for biosynthesis of taurine (Jacobsen & Smith, 1968).

The innovative description of the five pathways includes pathway 4, which is relevant to taurine biosynthesis in bacteria, while pathway 5 remains unsupported. Pathway 4 involves the inside transamination of isethionic acid. In teleosts, pathways 1 and 2 are likely predominant, depending on the species. In mammals, the activity of aspartate aminotransferase is significantly higher than that of cysteinesulfinic acid decarboxylase, resulting in the transamination of a majority of cysteine sulfinic acid. Key enzymes involved in these pathways include cysteinesulfinic acid decarboxylase (CSD), aspartate aminotransferase (AAT), cysteine dioxygenase (CDO), 2-aminoethanethiol dioxygenase (ADO), phosphoadenosine phosphosulfate (PAPS), and cysteic acid decarboxylase (CAD) (**Salze & Davis, 2015**)

According to Lavine, there is no considerable evidence to support pathway 5 because cysteine disulfide oxide is highly unstable and cysteine dissolves into sulfenate and cysteine. Later on, some investigators explained that the measured cystine disulfoxide was actually hypotaurine, this investigation rejected the former research that supported this pathway. Therefore, pathway V remains unproven. Pathway IV describes the biosynthesis of taurine by the inclusion of inorganic sulfate via cysteic acid and phosphoadenosine phosphosulfate (PAPS). Although it has been confirmed from evidence that pathway IV takes place in insects like cockroaches, it was shown that not insects themselves but bacterial endosymbionts play an essential role in the formation of cysteine from inorganic sulfur. In vertebrates, the defects of pathway IV were interestingly proved by radioisotope tracing. Despite that this pathway is referred to in several recently published literature, the formation of organic sulfur compounds from non-bacterial conversion of inorganic sulfate is usually recognized as irrelevant. Furthermore, some scientists assumed that for the *in vivo* synthesis of taurine, its deaminated form (Isethionic Acid) could be used. Nevertheless, no evidence was found for such a reaction; rather, the rate of this reaction is quite slow and considered as an opposite reaction. For many years, it has been clear that in mammals, the actual route for the biosynthesis of taurine was the cysteinesulfinic acid-dependent pathway (pathway I). However, about this pathway, two main points should be made. First, the flux of cysteine sulfur to taurine is primarily determined by the highly regulated cysteine dioxygenase (CDO). Changes in the availability of substrate are highly dependent on the activity of cysteine dioxygenase. Second, cysteinesulfinic acid can be either decarboxylated into hypotaurine or converted into  $\beta$ -sulfinylpyruvate. Both enzymes, cysteinesulfinic acid decarboxylase (CSD) and aspartate aminotransferase (AAT), have relative saturation constants  $K_m$ , which are responsible for these reactions and also determine the division between both of them, respectively. Because the  $K_m$  of aspartate aminotransferase is around 50 times greater than the  $K_m$  of cysteinesulfinic acid decarboxylase, cysteinesulfinic acid is mainly oxidized into  $\beta$ -sulfinylpyruvate instead of hypotaurine. Several studies indicate that birds depend on pathway II, such as when the formation of hypotaurine is not present

in chickens, they transform cysteine from cystic acid into taurine. Hypotaurine is formed during pathway III from decarboxylated cysteine (cysteamine). Though the evidence is not present for the activity of decarboxylated cysteine. Cysteamine is more probably generated by coenzyme A via the oxidation of pantothenic acid.

Early research on different fish species found no activity of cysteine sulfinate decarboxylase (CSD) in the Labridae, Scombridae, Soleidae families, and also the Rajidae. According to **Blaschko (1942)**, the activity of cysteic acid decarboxylase (CAD) was also low in the Gadidae family. **Yokoyama *et al.* (1992)** suggested that in some fish species like the tilapia and rainbow trout, greater activity of CSD was found. According to several studies, dietary taurine supplementation provides benefits to both the rainbow trout and tilapia, signifying that for the maximum development of fish, such concentrations of CSD activity are inadequate. This limited amount of CSD does not supply the required quantities of taurine for enhancing growth. Similarly, several observations suggested that in the species of the teleost, the limited production of hypotaurine occurs. Animals require dietary taurine for better development, as shown to be true for the red sea bream, Japanese flounder, and yellowtail. Cysteine dioxygenase (CDO) activity was increased after an intraperitoneal dose of cysteine. As a result, cysteine sulfinic acid was distributed equally between sulfate products and hypotaurine. It has been suggested that in the rainbow trout, taurine is generated through pathway-I. Nevertheless, in the species of the common carp, the production of hypotaurine was particularly limited, while the species is generally known to grow on a taurine-free diet. In addition, **Kim *et al.* (2005)** discovered that the common carp had a high ability to synthesize taurine. This shows that the common carp produces taurine via a different method rather than pathway I, likely pathway II, while the exact pathway is still unrecognized. Some other researchers found that adding the progesterin 17 alpha, 20 beta-dihydroxy-4-pregnen-3-one to the eel testis enhanced the synthesis of taurine through CDO up-regulation but not via CSD. This indicates that dietary taurine is synthesized via pathway II rather than pathway I. As a result, it's impossible to say that all the teleosts depend on pathway I for the production of dietary taurine.

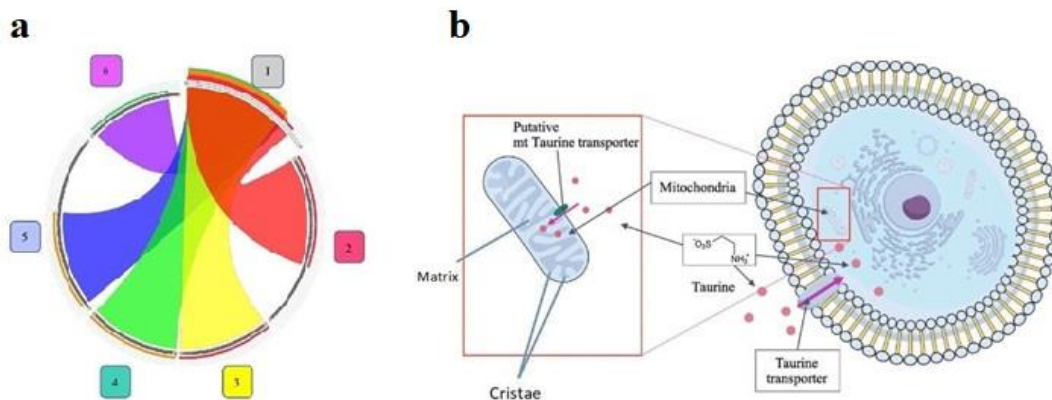
### **Transport of taurine**

Taurine is transported into the cell plasma from the intracellular plasma, along with cell plasma to mitochondria. A key gene that plays a pivotal role in this transportation is TauT (**Lombardini *et al.*, 1979**). Mainly, TauT facilitates the transport of taurine in cells and in mitochondria in fish, while also controlling the intracellular taurine accumulation. It enhances the synthesis of taurine in the liver by improving the efficiency of transportation within the cells. Recent studies have indicated that this gene contributes to the transportation of membrane taurine and to the biosynthesis of mitochondrial taurine (**Liu *et al.*, 2017**). According to the NCBI nucleotide database, the gene sequences of

TauT show a significant similarity among different species of fish. This suggests that taurine influences the expression of the TauT gene, providing an optimized transportation of taurine at the cellular level.

**Table 2.** Th conversion of cysteine in the liver of several fish species to taurine (**Goto *et al.* 2003**)

Name	Scientific name	Body weight	Activity (nmol/min per mg protein)
Carp	<i>Cyprinus carpio</i>	102–164 g	0.06 ± 0.07
Japanese flounder	<i>Paralichthys olivaceus</i>	0.6–3.0 kg	0.25 ± 0.13
Bluegill	<i>Lepomis macrochirus</i>	35-70 g	1.63 ± 0.55
Smelt fish	<i>Plecoglossus altivelis</i>	73-91 g	0.07 ± 0.04
Rainbow trout	<i>Oncorhynchus mykiss</i>	121–167 g	0.05 ± 0.08
Red sea bream	<i>Pagrus major</i>	1.0–1.5 kg	1.58 ± 0.96



**Fig. 4.** (a) Circos plot of TauT mRNA sequences resemblances among different species of fish according to 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 (**Sampath *et al.*, 2020**); (b) Biological pathway of Mitochondrial taurine transportation

### Physiochemical functions of taurine

Taurine plays a wide range of roles in mammalian physiology, but our understanding of its specific physiological functions in the teleost species is quite limited. However, taurine is considered a vital nutrient in several teleost species, and its deficiency has been associated with low survival rates and limited growth. These signs

hint at the importance of taurine although the exact role remains unclear. In many fish species, taurine deficiency can lead to high mortality rates, the development of green liver syndrome, and decreased hematocrit values, which are often linked to a reduced disease resistance (**Takagi *et al.*, 2006a**). Green liver syndrome is believed to occur due to the overproduction of hemolytic biliverdin and a decrease in bile pigment excretion caused by dietary taurine deficiency. Taurine's effects on membrane stability and osmoregulation in various fish species appear to play a crucial role in suppressing the hemolysis (**Takagi *et al.*, 2006b**). When taurine is insufficient or absent in fish diets, it can lead to histological changes and various physiological disorders. This study primarily focused on exploring the effects of taurine on physiological processes, such as growth and metabolism in different fish species.

### **Effect on growth**

The deficiency of taurine in the diet often manifests as growth depression, a symptom commonly observed in various conditions. However, growth depression alone is not a sufficient evidence to diagnose taurine deficiency. The growth of a species is influenced by the availability of nutrients obtained from metabolic expenditure, which are deposited in the body tissues. These depositions are essential for various functions such as digestion, reproduction, and maintenance. Some free amino acids, including taurine, have been shown to increase appetite, leading to increased feed consumption and subsequently, growth (**Kasumyan & Doving, 2003**). However, the effect of taurine on growth can vary among different fish species.

Studies have reported that taurine supplementation can stimulate appetite and increase feed consumption in some species, resulting in an improved growth. Conversely, in other species such as the grass carp, taurine supplementation may not have a significant stimulant effect on appetite or growth (**Yang *et al.*, 2013**). Taurine's osmoregulatory effect has also been demonstrated in fish, with supplementation leading to an increase in skin thickness, indirectly affecting osmoregulation (**Kato *et al.*, 2014**).

Changes in body structure may also occur in response to dietary taurine levels, but caution must be exercised when comparing studies conducted with different species, food sources, and husbandry conditions. Generally, a restricted level of taurine in the diet tends to decrease the lipid content of the body although there are exceptions such as in the rodents and Atlantic salmon, where the opposite trend has been observed (**Espe *et al.*, 2012**).

In some fish species like the Nile tilapia, juvenile carp, and grass carp, dietary taurine supplementation has been shown to improve growth rates (**Li *et al.*, 2005; Liu *et al.*, 2006**). For example, the supplementation of taurine in the diet of the juvenile

Japanese flounder enhanced their growth rate (**Kim *et al.*, 2005**). However, the optimal taurine concentration in the diet for a maximum growth varies among species.

Interestingly, in the channel catfish, dietary taurine supplementation did not have any significant influence on growth. Similarly, in the grouper, while taurine supplementation from soybean meal improved growth efficiency, excessive levels of taurine in the diet did not result in higher weight gain compared to a diet with precise taurine concentrations (**El-Sayed, 2013**). These findings highlight the complex relationship between dietary taurine supplementation and growth in different fish species.

**Table 3.** In larval teleosts, a list of species and important reactions compiled to taurine

Species	Diet/live prey (enrichment method)	Dietary taurine content, % diet	Primary response criteria	Recommended supplement (% diet)	Ref.
Japanese flounder <i>Paralichthys olivaceous</i>	Ro (dTau)	Ro: 0.09–0.45%, dm	Growth	R	( <b>Chen <i>et al.</i> 2005</b> )
Yellowtail <i>Seriola lalandi</i>	Ro (dTau)	Enriched	Survival, Growth	R	( <b>Chen <i>et al.</i> 2004</b> )
Red Sea bream <i>Pagrus major</i>	Ro (dTau)	Ro: 0.11–0.32%, dm	Growth	R	( <b>Rotman <i>et al.</i> 2017</b> )
White Seabass <i>Atractoscion nobilis</i>	Ro (dTau)	Enriched	Survival, Growth	?	( <b>Rotman <i>et al.</i> 2017</b> )

Ro: rotifer; dTau: crystal taurine dissolved in enrichment medium; dm: dry-matter basis; R: required; Ref: Reference.

Table (3) summarizes the outcomes of taurine supplementation in the diet of the larvae, with a focus on the carnivorous species commonly used in larval investigations. These species are challenging to rear due to their tiny size. Dietary taurine supplementation has shown benefits across various species, including improved survival and growth rates, an enhanced digestive enzyme activity, and a morphological development, with the exception of the white seabass and red sea bream (**Koch *et al.*, 2016**).

Recent studies have concentrated on understanding the effects of dietary taurine supplementation on the Nile tilapia, particularly on growth, feed efficiency, and reproduction rates (**Koch *et al.*, 2016**). Notably, studies have limited knowledge about the

impact of dietary taurine on the physiology and metabolism of the Nile tilapia (**Wang & Lu, 2016**).

In the case of the juvenile pirarucu, dietary taurine supplementation did not positively influence growth but also did not have any negative effects, suggesting that the species' growth may have been supported by the baseline diet concentrations of methionine and taurine (**López et al., 2015**). Taurine supplementation in the diet of the totoaba juveniles has been shown to improve the growth in this species (**López et al., 2015**).

A substantial body of research indicates that fish growth is significantly enhanced by dietary taurine supplementation ranging from approximately 0.5 to 1.5 percent. Moreover, taurine supplementation has been found to increase the survival rates in larvae and enhance egg fertility in broodstock (**López et al., 2015**).

Various studies have sought to determine the optimal taurine content in the red seabream diets. For instance, during periods of low water temperature, supplementation of 1 percent dietary taurine alongside soybean meal up to 35 percent has been shown to improve the feed utilization and growth rates in the red seabream (**Martins et al., 2018**). **Matsunari et al. (2008)** suggested that the juvenile red seabream fed a casein-based diet require 0.5 percent taurine. Additionally, recent studies have indicated that the required amount of dietary taurine in the red seabream diets varies across growth phases and depending on the primary protein source used in the diets, ranging from 0.5 to 2 percent (**Salze & Davis, 2015**).

### **Effect on metabolism**

Various studies demonstrate that supplementation of taurine plays a key role in altering metabolism in different fish species, such as the juvenile red seabream, turbot (*Scophthalmus maximus*), juvenile yellow catfish, totoaba (*Totoaba macdonaldi*), the Nile tilapia, grouper (*Epinephelus coioides*), juvenile black carp, etc. (**López et al., 2015; Salze et al., 2016; Wang & Lu, 2016**).

Dietary taurine supplementation performs various significant roles in the metabolic functions of fish, such as bile acid formation and osmoregulation although our understanding of taurine's effects on metabolic functions remains limited (**Wang & Lu, 2016**).

In the teleost species, practically all known bile acid conjugations originate with taurine, and many aquaculture-relevant species excrete solely the C24 bile acids chenodeoxycholic acid and cholic acid (**Hofmann et al., 2010**). However, some exceptions exist, such as the paddlefish and sturgeons, which have high quantities of C27 bile alcohol, and the cyprinids, which have 5-cyprinol sulfate as the major bile salt (**Hofmann et al., 2010**).

Empirical findings suggest that the supplementation of dietary taurine increases the bile salt content in various teleosts, leading to improvements in growth, lipid digestion, and morphology of the distal part of the intestine in the rainbow trout species (**Matsunari *et al.*, 2008; Howard & Udenigwe, 2013**).

However, the supplementation of taurocholic acid was inadequate for species like the red seabream (*Pagrus major*) in the complete recovery of the bile salt concentration and growth during taurine supplementation (**Matsunari *et al.*, 2008**).

Some previous studies revealed that water temperature affects the metabolic rate of the red seabream, but the impacts of low water temperature on the red seabreams have not been adequately investigated (**Woo, 1990**).

### **Metabolism of lipid**

About alterations in lipid metabolism, some studies reported that taurine supplementation may increase the activity of CYP7A1, a rate-limiting enzyme, stimulating cholesterol conversion into the bile acid and proceeding lipid synthesis (**Gaylord *et al.*, 2006**). It has been suggested that lipid metabolism may be enhanced by the rise in glycerol phosphocholine and choline phosphorylcholine from the non-gravid stage of the juvenile tilapia to the middle and late feed phases (**Gaylord *et al.*, 2006**). Moreover, cholate is commonly conjugated with taurine or glycine to aid cholesterol excretion and fat absorption (**Gaylord *et al.*, 2006**). These metabolic alterations imply that taurine may stimulate the synthesis of protein and lipid in fish, consistent with the elevation in crude lipid and crude protein in the fish body (**Gaylord *et al.*, 2006**).

In the juvenile yellow catfish (*Pelteobagrus fulvidraco*), increasing dietary taurine up to 2.55 percent significantly reduced the levels of cholesterol and triglycerides in all-plant protein diets (**Li *et al.*, 2016**). In the zebrafish (*Danio rerio*) and totoaba (*Totoaba macdonaldi*), dietary taurine supplementation reduced the lipid peroxidation in the liver (**Rosemberg *et al.*, 2010; Bañuelos-Vargas *et al.*, 2014**). Furthermore, dietary taurine enhanced the grouper (*Epinephelus coioides*) lipid metabolism by improving metabolic control and lipid digestion (**Shen *et al.*, 2019**).

Hence, taurine is involved in a variety of lipid metabolic processes in fish, including the bile acid production, lipid digestion, emulsification, and fat deposition and absorption (**Gaylord *et al.*, 2006**).

### **Metabolism of protein**

Dietary taurine supplementation enhanced the amount of protease in the common carp (*Cyprinus carpio*) (**Abdel-Tawwab & Monier, 2018**). In the juvenile European sea bass (*Dicentrarchus labrax*), dietary taurine enhanced the ratio of protein efficiency by 1.2 percent, while having no effect on the whole-body protein content (**Martins *et al.*, 2018**).



Nevertheless, dietary taurine content boosted the whole-body protein content of the cobia (*Rachycentron canadum*) (Watson *et al.*, 2013). Furthermore, the supplementation of dietary taurine in the grouper (*Epinephelus coioides*) enhanced the synthesis of protein and amino acid absorption through metabolic regulation action in the protein synthesis pathway (Shen *et al.*, 2019). Thus, metabolism of protein improved by dietary taurine in various fish species.

### Metabolism of amino acids

Taurine has a greater impact on amino acid metabolism than other amino acids (Li *et al.*, 2009). In the muscles of the Nile tilapia (*Oreochromis niloticus*), the concentration of amino acids, such as proline, methionine, lysine, histidine, glycine, leucine, and alanine, were all reduced after taurine supplementation. These alterations in metabolic activities are linked to changes such as amino acid production, mineral absorption, and the absorption and digestion of protein (Matsunari *et al.*, 2008). An increase in the level of taurine supplementation caused a decline in the levels of glycine, alanine, and proline, similar to previous studies on the milkfish (*Chanos chanos*) (Shiau *et al.*, 1997), yellowtail (Takagi *et al.*, 2006b), and the red sea bream (Matsunari *et al.*, 2008). As a result, amino acid levels decrease due to taurine supplementation while speeding up growth and gluconeogenesis in the fish's body.

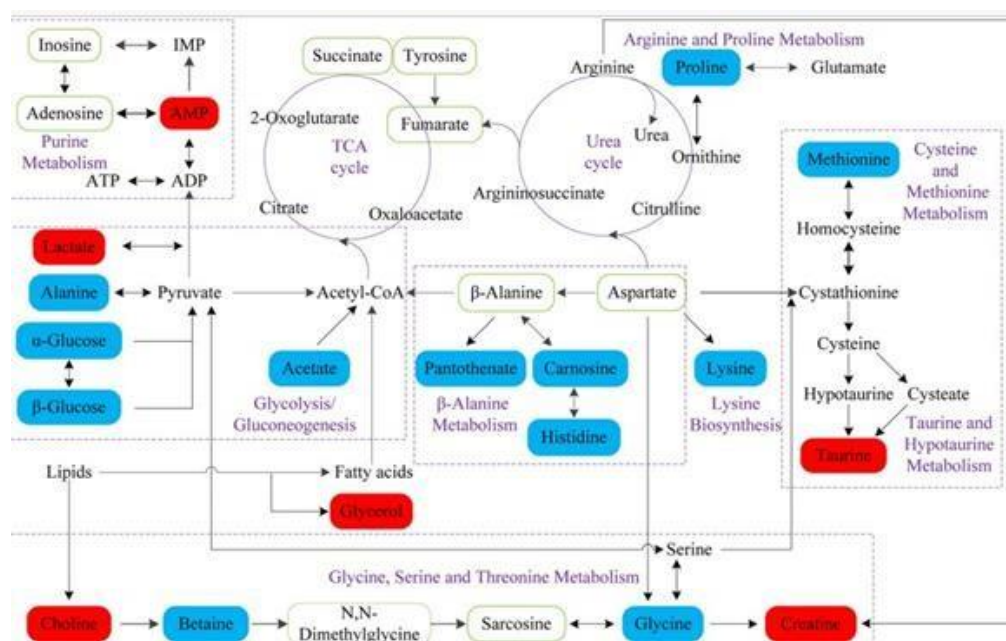
### Metabolism of carbohydrates

The capacity of carbohydrate metabolism in fish is primarily determined by factors, such as glucose transport rate, insulin receptors, enzyme activity, and hepatic glucose utilization. In studies on the common carp (Abdel-Tawwab & Monier, 2018), black carp (*Mylopharyngodon piceus*) (Zhang *et al.*, 2018), and turbot (Zhang *et al.*, 2019), dietary taurine supplementation boosted the intestinal amylase activity. In turbot plasma, the synergistic effects of carbohydrates and dietary taurine drastically reduced the fructose-1,6-bisphosphate gene expression and glycation end-products (Zhang *et al.*, 2019). Conversely, the gene expressions of various enzymes involved in carbohydrate metabolism, such as glucokinase, phosphofructokinase, pyruvate kinase, glucose-6-phosphate dehydrogenase (G6PD), glycogen synthase (GS), and glucose transporter 2, were significantly increased. Taurine supplementation also enhanced the glucose tolerance in the turbot (Zhang *et al.*, 2019), while reducing the expression of liver cytosolic phosphoenolpyruvate carboxykinase (cPEPCK) (Zhang *et al.*, 2019). Moreover, taurine reduces catabolic enzymatic activity in the gluconeogenesis pathway (Bañuelos-Vargas *et al.*, 2014) and interacts with insulin receptors to lower blood glucose levels, as observed in the white seabream (Magalhães *et al.*, 2019).

In the Nile tilapia, adenosine monophosphate (AMP), lactate, glycine, and alanine are involved in glycolysis and gluconeogenesis pathways. The rise in the AMP may be linked to the increased hydrolysis of ATP, providing the necessary energy for fish

development (Shao *et al.*, 2015). The increase in lactate suggests an accelerated anaerobic glycolysis in fish muscles, likely due to the rapid growth requiring significant energy utilization at both early and later stages (Shao *et al.*, 2015). Alanine serves as a glucogenic precursor in fish (Li *et al.*, 2014).

Furthermore, carnosine has the ability to reduce various metabolic alterations such as glycation and protein oxidation, acting as a buffer in the skeletal muscles of marine organisms, particularly the migratory pelagic marine fishes (Blancquaert *et al.*, 2016). The alteration in energy metabolism suggests that taurine supplementation boosts energy consumption in muscle tissues, likely due to improved metabolic processes such as protein synthesis and lipid metabolism (Wang *et al.*, 2016).



**Fig. 5.** Dietary taurine affecting metabolic pathways in the tilapia muscle extracts (Shen *et al.*, 2018)

## CONCLUSION

The extensive body of research suggests that dietary taurine supplementation significantly promotes the growth of fish and serves as a fish feed activator across various species. Taurine supplementation impacts not only growth but also muscle texture, metabolic functions, feeding behavior, and fish immunity. The emergence of green liver syndrome in the red sea bream is attributed in part to taurine deficiency although the full extent of its effects remains incompletely understood. Taurine deficiency can lead to high mortality rates, low feed efficiency, and anemia in various fish species. While taurine is

considered a weak stimulant in the red sea bream, its supplementation has significant effects on the growth and physiological activities in fish species overall. The activity of cysteinesulphinate decarboxylase (CSD) is crucial in taurine biosynthesis, emphasizing its importance in fish nutrition. This review underscores the need for further research into the roles of dietary taurine in various fish species, particularly focusing on the juveniles, the cichlids (such as the Nile tilapia), and the teleost fish. Despite its importance, the function of taurine in basic metabolic activities in fish remains poorly understood. Therefore, more comprehensive studies are warranted to elucidate the effects of taurine on different species of fish at various life stages. To advance fish nutrition and optimize taurine supplementation strategies, further research on sulfur amino acid metabolism and the physiological activities of taurine in fish is recommended. This would contribute to a better understanding of the intricate mechanisms underlying taurine's effects on fish physiology and growth, ultimately enhancing fish health and aquaculture practices.

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