

Chapter 11

Taurine—‘Controlling Rather than Fueling’



Abstract Taurine is an amino acid that differs from the more familiar AAs in possessing a sulfonic rather than a carboxylic group. It is central in membrane stabilization, antioxidation, detoxification, immune response, calcium transport, myocardial contractility, retina development, bile acid metabolism, and endocrine functions. It comprises up to 50% of the free AA pool and is central in osmoregulation. Tau is an essential nutrient in many aquatic animals. Appropriate Tau supplementation sustains many health and metabolism aspects and endurance of farmed fish, while excess Tau seems to be “toxic” to shrimps and fishes. Dietary Tau increases phagocytic activity as well as innate immunity by upregulation of immunity gene transcription. Many details of the metabolism of dietary normal and excess Tau have been identified only phenotypically; details remain to be proven by innovative biomolecular approaches. Furthermore, the role of the intestine microbiota in Tau metabolism has not yet been considered appropriately.

In addition to the proteinaceous amino acids (AAs) described in previous chapters, another major AA, taurine (Tau, Fig. 11.1a), plays an overwhelming controlling role in animals (Laidlaw et al. 1990). Tau is an AA that differs from the more familiar ones in being a sulfonic rather than a carboxylic AA and in being a β -AA rather than an α -AA. Compared with carboxylate groups, the sulfonate group is a strong acid (Huxtable 1992).

The replacement of the carboxyl group by the sulfonate group disables the molecule to form peptide bonds; hence, Tau can usually not be part of peptide chains. Consequently, Tau is the most abundant free AA in animal tissues, accounting for up to 25% of the free AAs pool in the liver, 50% in the kidney, 53% in the muscle, and 19% in the brain (Salze and Davis 2015). Tau plays significant roles in membrane stabilization, antioxidation, detoxification, immune response, calcium transport, myocardial contractility, retina development, bile acid metabolism, and endocrine functions (El-Sayed 2014)—at least in mammals.

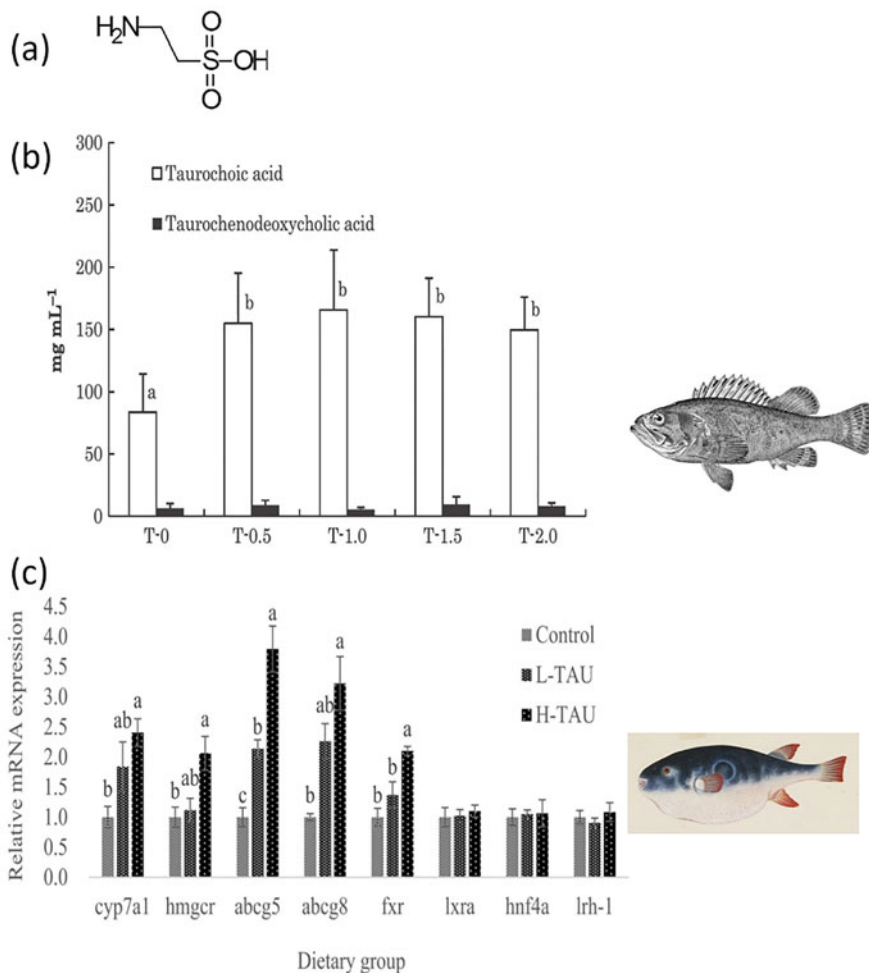


Fig. 11.1 (a) Taurine (=2-aminoethanesulfonic acid). (b) Conjugated bile acids detected in gallbladder bile of juvenile Korean rockfish (*Sebastes schlegelii*) at the end of the 4-month feeding study. **T-0** to **T-2.0**: diets with increasing Tau content (0.7 to 17 mg g⁻¹ dry matter). Different superscripts indicate significant differences ($P < 0.05$). (From Kim et al. (2015), with permission from Wiley). (c) Relative mRNA expression of genes related to bile acid and cholesterol metabolism in the liver of tiger puffer (*Takifugu rubripes*). Different superscripts indicate significant differences ($P < 0.05$). (From Xu et al. (2020), with permission from the Cambridge University Press; images credit Naturalis Biodiversity Center). L-TAU 8 g kg⁻¹ diet; H-TAU 14 g kg⁻¹ diet; *cyp7a1* cholesterol 7 α -hydroxylase; *hmgcr* 3-hydroxy-3-methylglutaryl-CoA reductase; *abcg* ATP binding cassette subfamily G; *fxr* farnesoid X receptor; *lxra* liver X receptor α ; *hnf4a* hepatocyte nuclear factor 4 α ; *lrh-1* liver receptor homolog-1

Since Tau comprises up to 50% of the free AA pool, it plays a role in osmoregulation as shown in:

- Marine fishes: European flounder (*Platichthys flesus*), winter flounder (*Pseudopleuronectes americanus*), and little skate (*Leucoraja erinacea*).
- Brackish fishes: mangrove killifish.
- Freshwater fishes: walking catfish, tilapia, and common carp (Fugelli and Zachariassen 1976; Frick and Wright 2002; Chara et al. 2011).

The osmoregulatory function of Tau applies also to euryhaline invertebrates in intertidal ecosystems, such as penaeid shrimps *Marsupenaeus japonicus*, *Penaeus monodon* (Richard et al. 2011), and *Litopenaeus vannamei* (Li et al. 2017), prawns *Palaemon elegans*, bivalves *Mytilus galloprovincialis* (Ji et al. 2013) and *Ruditapes philippinarum* (Liu et al. 2013), and the freshwater giant shrimp *Macrobrachium rosenbergii* (El-Sayed 2014). Another proof of the osmoregulatory activity of Tau is the increase in Tau transporter (*tauT*) mRNA in carp and tilapia tissues during salinity-induced stress (Takeuchi et al. 2000a, b). Consequently, in maintaining the osmotic homeostasis, the sufficient dietary supply with Tau or its precursors is central (Chara et al. 2011).

Except of spontaneous basic physiological functions, such as antioxidation or osmoregulation, the functions of Tau in fishes and aquatic invertebrates are much less well documented than in mammals. In teleost species where Tau has been identified as an essential nutrient, poor growth and reduced survival are consistently observed during Tau deficiency. However, such phenotypic symptoms are uninformative to the roles of Tau (Salze and Davis 2015) and still subject to extensive studies. As effective antioxidant in aquatic animals (Zhao et al. 2017), Tau counteracts oxidative stresses by scavenging reactive oxygen species (ROS) that are produced as multipurpose tools after the impact of different internal as well as external stressors (Steinberg 2012).

Tau accelerates growth and improves immunity and survival of fish larvae (Kim et al. 2016). Furthermore, it is involved with several important biological functions including fat digestion as a conjugator with bile acids, such as cholic acid or chenodeoxycholic acid in the liver (Fig. 11.1b), and stimulates the hepatic biosynthesis of both bile acid and cholesterol (Fig. 11.1c).

11.1 Taurine Biosynthesis and Physiology

Over the past decade, it has become obvious that Tau is an essential nutrient in many aquatic animals, as shown in octopus (Lopes et al. 2016), sea cucumber (Liu et al. 2016), shrimps (Yue et al. 2013; El-Sayed 2014), and fishes (El-Sayed 2014; Salze and Davis 2015; Magalhães et al. 2019). Meanwhile, several endogenous biosynthesis pathways have been discussed (see below); however, numerous fish species benefit from dietary Tau supplementation, thus showing that the two endogenous pathways are insufficient to provide the necessary amounts of Tau for maximal

growth (Salze and Davis 2015). In this review, the authors summarize the recommended Tau supplement for various fish species from dietary 0.2% (common dentex, *Dentex dentex*; European seabass; rainbow trout) to 1.7% (Japanese flounder).

In larval cobia, Salze et al. (2012) found that Tau supplementation increases specific amylase and trypsin activities in early stages, later also lipase and pepsin. These increased enzymatic activities lead to enhanced nutrient availability, thus providing some explanation to the improved development, growth, and post-weaning survival observed in Tau-supplemented larvae.

Moreover, Tau is an important neurochemical factor in the animal visual system. Abundant Tau is localized in the retinal photoreceptor and neural layers of, for instance, the anadromous ayu (*Plecoglossus altivelis*), juvenile Japanese flounders, glass eel, and young goldfish (Omura et al. 1997; Omura and Yoshimura 1999; Nusetti et al. 2006, 2010), demonstrating that Tau is involved in the protection of the photoreceptor outer segment, the regulation of neural transmission, and photoreceptor differentiation.

The Tau biosynthetic pathways have been the subject of research for several decades, in spite of which some parts remain poorly characterized. The cysteinesulfinate-decarboxylase (CSD) pathway is the main pathway in mammals. CSD activity occurs in freshwater fishes, such as rainbow trout, common carp, tilapia, bluegill (*Lepomis macrochirus*) as well as Atlantic salmon (El-Sayed 2014); however, the activity remains an order of magnitude lower than in small mammals. Furthermore, studies with common carp indicate that this species relies on a different pathway than the CSD pathway for Tau production, possibly the pathway using cysteic acid decarboxylase; the precise pathway, however, remains to be ascertained (Salze and Davis 2015). Consequently, one cannot systematically assume that all teleost rely on the CSD pathway for the biosynthesis of Tau. Recently, Ma et al. (2021) found that golden pompano (*Trachinotus ovatus*) possesses the key enzyme for Tau biosynthesis through two main pathways, and exogenous Tau intake directly affects the expression of synthesis-related genes in the liver. Tau biosynthesis alone, however, is insufficient to satisfy the demands of *T. ovatus*; the results indicate that approximately 10 g kg^{-1} of Tau still needs to be provided via diet.

Tau is mainly synthesized in the fish liver. Consequently, the liver is the most-impacted organ in the event of deficiencies. Green liver syndrome is arguably the most specific symptom of Tau deficiency. The green liver originates from the accumulation of biliverdin and reduced excretion of bile pigment from the liver to the bile (Salze and Davis 2015). Tau supplementation effectively reduces the severity of green liver disease in yellowtail fed a diet devoid of fishmeal and containing less than 0.1% Tau (Takagi et al. 2005). This indicates that Tau deficiency can be at the origin of this nutritional disease.

As mentioned, Tau is a major compound of bile and central in lipid metabolism via bile acids. Bile acids are steroids derived from cholesterol, synthesized in the liver, stored in the gallbladder, and released into the intestinal lumen to emulsify fats and help in the absorption of lipids and fat-soluble vitamins. Bile acids are

conjugated mainly with Tau and—to a lesser extent—with Gly. Therefore, Tau enhances lipid metabolism in fishes, through increase in the bile salt-activated hepatic lipase activity. Therefore, Tau as well as bile salts can be used as olfactory stimuli to increase feed uptake as documented in European glass eel, European seabass fry, gilthead seabream fry as well as rainbow trout, and channel catfish (El-Sayed 2014; Jirsa et al. 2014).

Less well understood is the Tau biosynthesis in invertebrates. The enhanced growth of *P. monodon* after dietary addition of Tau indicates limited Tau endogenous synthesis in this shrimp (Shiau and Chou 1994). More recently, Richard et al. (2011) showed that *P. monodon* has a capacity to regulate Tau synthesis in relation to dietary Cys2 levels. In contrast to *P. monodon*, the giant river shrimp (*M. rosenbergii*) appears to cover its Tau requirement by biosynthesis (Smith et al. 1987). However, in both shrimps, details of the biosynthesis pathway remain to be discovered.

Tau is absorbed by the intestinal epithelium through a specific, Na^+/Cl^- -dependent Tau transporter (TauT). In mammals, compounds are identified to inhibit specifically the uptake of Tau in the intestine, particularly β -alanine. These substances can be classified as anti-nutritional factors (Salze and Davis (2015)). TauT is found, for instance, in common carp and tilapia, Senegal sole, Mediterranean blue mussel, and Pacific oyster (Hosoi et al. 2005, 2007). However, information of anti-nutritional substances is lacking; but a deeper understanding of the interactions between these antinutrients (alone or in combination) with Tau—and other nutrients—in respect to bioavailability and metabolism would be invaluable to refine requirement estimates and necessary supplementation levels (Salze and Davis 2015). Furthermore, it has to be evaluated which other factors affect the Tau transport. In addition, it is also unexplored whether the transcription of transporter genes underlies a diurnal rhythmicity itself as it is well understood from genes encoding detoxification enzymes, such as cytochrome P-450 monooxygenases or glutathione transferases (Hooven et al. 2009; Brager et al. 2011) (for more detail, →AAN I “Chrononutrition” (Steinberg 2018)).

In Nile tilapia muscle, Shen et al. (2018) visualized the metabolic trajectory and revealed the metabolic mechanisms of dietary Tau supplementation on growth. Nineteen Tau-induced metabolic changes are involved in carbohydrate, AA, lipid, and nucleotide metabolism; Tau has a central metabolic position (Fig. 11.2). This paper presents pathways and supports the notion that Tau supplementation significantly regulates growth and development.

In a series of papers, Pinto and coworkers demonstrated the role of Tau in gilthead seabream larvae. The essentiality for Tau appears not to exist; this species can grow on Tau-free diets, since it biosynthesizes Tau from Met. However, Tau dietary supplementation may beneficially affect larval metabolism by increasing Met availability for several other important physiological purposes in the one-carbon metabolism (Pinto et al. 2013a).

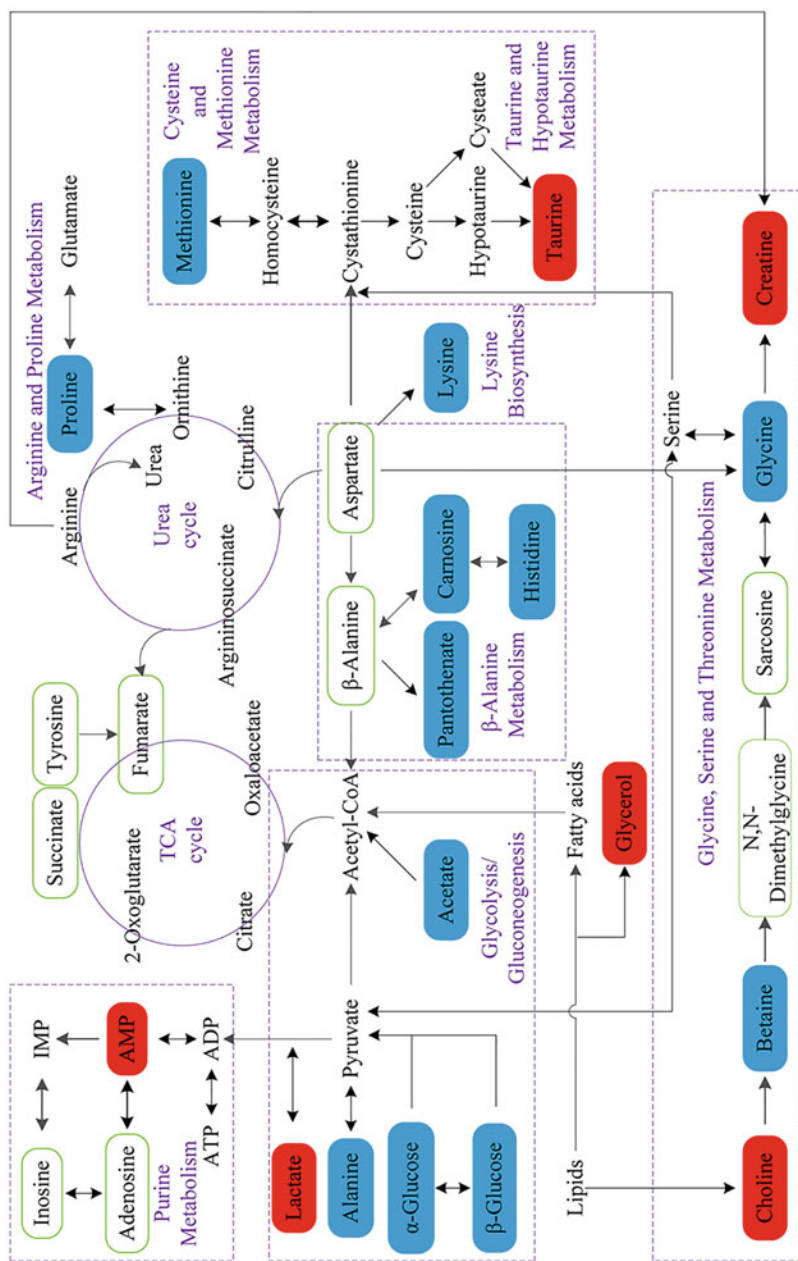


Fig. 11.2 Metabolic pathways affected by dietary Tau in tilapia muscle extracts. Metabolites in red and blue represent higher or lower levels in tilapia muscle extracts of the Tau-supplemented groups, when compared with the control group. Metabolites in green frames represent nonsignificant change and were detected by ^1H NMR, and metabolites with no color marking were not detected. (From Shen et al. (2018), with permission from the American Chemical Society)

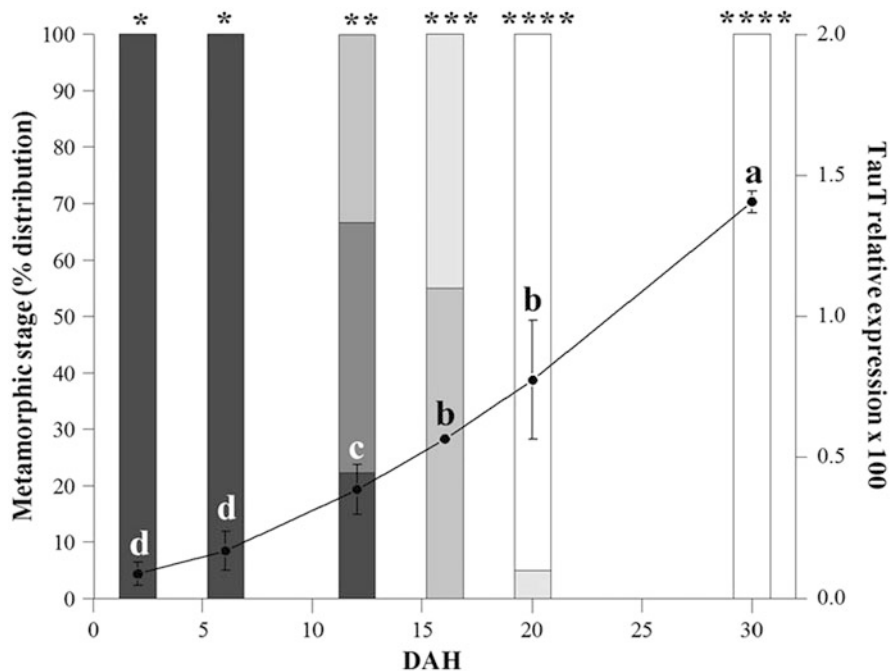


Fig. 11.3 Metamorphosis pattern and *tauT* expression in *Solea senegalensis* larvae. **DAH** days after hatching (=dph). Results for metamorphosis pattern are expressed as percentage of each metamorphic stage (Pre-■; Early■, Middle□,□, and Late□). Results for *tauT* expression (—●—) are given as means ± SD. Asterisks represent significant differences for the mean metamorphic stage at a certain age. Different letters represent significant differences for the expression of the *tauT* throughout larval development. (From Pinto et al. (2013b), with permission from Springer Nature)

In contrast to gilthead seabream, flatfishes, such as the Senegalese sole, require dietary Tau. Flatfishes undergo a visibly marked metamorphosis. Pinto et al. (2013b) assessed the effect of Tau supplementation in sole larvae and juveniles via growth, metamorphosis success, AA metabolism, and transcription of *tauT*. The transcription increases during larval development, increasing at the onset of metamorphosis (12 days after hatching, DAH) and achieving the highest values at post-metamorphosis (30 DAH; Fig. 11.3). In Senegalese sole juveniles, *tauT* mRNA is ubiquitously expressed in all analyzed tissues, with high expression in the brain, heart, and eye. In the digestive tract, high *tauT* expression occurs in hindgut and stomach tissues, indicating that dietary Tau is readily absorbed when the digestive process begins. Furthermore, Tau endogenously used for bile salt conjugation can be reabsorbed at the posterior end of the digestive tract pointing out the presence of an enterohepatic recycling pathway for Tau in Senegalese sole, at least in the juvenile stage. This process appears to be important for the maintenance of the Tau pool in the body—likely not only in this but also in other flatfish species.

Furthermore, Tau induces important protective biochemical mechanisms. In the liver and anterior intestine of European seabass, stress protein levels and the MAPK¹ pathway as well as lactate dehydrogenase are upregulated (Feidantsis et al. 2014). Furthermore, dietary Tau increases immunity and resistance against hyperammonemia in juvenile yellow catfish (Li et al. 2016) pointing out that appropriate Tau supplementation sustains health and endurance of farmed fish.

In many fishes, replacement of marine proteins with plant proteins leads to reduced growth (Espe et al. 2012) and development of enteritis. Plant ingredients are low in Tau (Liaset and Espe 2008); and thus Tau is conditionally indispensable if the plant ingredients become the main protein source in aquafeeds. Several studies exist in which either voluntary feed intake or growth performance improves following exogenous Tau addition to diets based on non-marine protein ingredients. However, in juvenile Atlantic salmon, the addition of 0.1% Tau to high plant protein diets has an adverse effect on growth (Espe et al. 2012). It decreases the lipid content in the entire fish, without affecting protein accretion, and thus reduces the body lipid-to-protein ratio and increases the liver pool of free AAs. A decreased lipid deposition is also observed in Japanese flounder after Tau supplementation (Han et al. 2014). Taken together, the partitioning of growth and nutrient deposition pattern following the availability of sulfur AAs, including Tau, has to be studied in more detail because such knowledge can facilitate the production of slimmer and healthier fish during the growth period, in which the majority of fat deposition occurs.

Some more studies of dietary Tau effects in farmed animals are listed in Table 11.1. The results span from inconspicuous to beneficial effects. Many studies replace fishmeal by plant-based proteins and supplement Tau.

Supplementing 3.5% Tau in an all-plant protein diet, Hu et al. (2018) showed that this AA is a phagostimulant in large yellow croaker (*Larimichthys crocea*) and upregulates a variety of olfactory receptor genes in the olfactory epithelium (Fig. 11.4). The phagostimulation aids the development of an all-plant protein feed for this fish. Moreover, Tau-enriched rotifers and *Artemia nauplii* fed to gilthead seabream larvae have beneficial effects on retinal opsin abundance and gene expression of five main opsins. The Tau effect on the pattern of gene expression of selected opsins in the larvae is age-dependent and potentially improved vision leading to increased hunting success and weight gain (Gaon et al. 2020).

Dietary Tau mitigates oxidative stress and apoptosis at low temperatures as shown in obscure pufferfish (*Takifugu obscurus*) (Fig. 11.5). Apoptosis is a form of programmed cell death that occurs in multicellular organisms (Elmore 2007), and caspases are its executioners. Caspase-3 is the major player responsible for the proteolytic cleavage of many critical cellular proteins (Elmore 2007). Dietary Tau

¹Mitogen-activated protein kinases are involved in directing cellular responses to a diverse array of stimuli, such as mitogens, osmotic stress, heat shock, and pro-inflammatory cytokines. They regulate cell functions including proliferation, gene expression, differentiation, mitosis, cell survival, and apoptosis (Pearson et al. 2001).

Table 11.1 Recent effect studies of dietary taurine in aquatic animals

Species	Diet	Dietary Tau level, %	Effects	References
Invertebrates				
<i>Eriocheir sinensis</i> , Chinese mitten crab	Regular diet	0→1.6	WG↑, immunity↑, AOC↑ Optim @ 0.4–0.8	Dong et al. (2018)
<i>Penaeus monodon</i> , black tiger shrimp	41% P	1.5	Feeding attractant→SGR↑	Hartati and Briggs (1993)
Fishes				
<i>Acanthopagrus latus</i> , yellowfin seabream	Low FM diet	0→1.6	SGR↑, FCR↑ optim ~1.1	Dehghani et al. (2020)
<i>A. schlegelii</i> , black seabream	All-plant diet	0→2.0	WG↑, cholesterol→bile acid ^a <i>cyp7a1</i> ↑	Tong et al. (2019)
			Serum protein↑, serum cholesterol↓, hepatic bile acid↓	Tong et al. (2020)
<i>Argyrosomus regius</i> , meagre	High plant diet	0, 1.0	WG↔, FCR↔	de Moura et al. (2018)
<i>Clarias gariepinus</i> , African catfish		0→4.0	WG↑, FCR↔	Adeshina and Abdel-Tawwab (2020)
<i>Ctenopharyngodon idella</i> , grass carp		0→0.2	WG↑, intestinal health↑	Yan et al. (2019)
<i>Cyprinus carpio</i> , common carp	Regular diet	0→2.0	Salinity stress resistance↑, optim @ 1.5	Abdel-Tawwab and Monier (2018)
<i>Danio rerio</i> , zebrafish	High plant diet	0→1.5	WG↔, reproduction↔	Guimarães et al. (2018)
<i>Dicentrarchus labrax</i> , European seabass	Low FM diet	0, 0.26	AOC(↑)	Coutinho et al. (2017)
		1.5	WG↑, ROS↓, liver <i>cat</i> ↓, muscle <i>gpx</i> ↓	Ceccotti et al. (2019)
		0, 1.5, 5.0	Spectral sensitivity↓	Brill et al. (2019)
		0, 1.0	WG↑, AOC↑, <i>casp3</i> ↓, <i>casp9</i> ↓, inflammation↓, lipogenesis↓, β-oxidation↓, <i>cyp7a1</i> ↔	Martins et al. (2019, 2021)
	Low FM diet; 32% soy	0→1.0	Growth↔	Kotzamanis et al. (2020)
FM-based	1.0	Growth↑, immunity↑	Saleh et al. (2020)	

(continued)

Table 11.1 (continued)

Species	Diet	Dietary Tau level, %	Effects	References	
<i>Larimichthys crocea</i> , large yellow croaker	All-plant protein diet	3.5	Phagostimulation \uparrow , <i>olfactory receptors</i> \uparrow (Fig. 11.4)	Hu et al. (2018)	
<i>Lates calcarifer</i> , barramundi	Plant-based diet	0.1 \rightarrow 1.5	Growth \uparrow , if S-AAs deficient	Poppi et al. (2018)	
<i>Oreochromis niloticus</i> , Nile tilapia	Soy-based diet	0 \rightarrow 1.0	Met sparing	Michelato et al. (2018)	
<i>Rachycentron canadum</i> , cobia	Plant-based diet	0.5	WG \uparrow	Raggi et al. (2019)	
<i>Scophthalmus maximus</i> , turbot		0.8	WG \leftrightarrow	Wei et al. (2019)	
		Low FM diet	0 \rightarrow 2.0	Muscle growth \uparrow , collagen \uparrow	Wijerath Wiriduge et al. (2020)
		15% carbohydrates		WG \uparrow , hepatic AOC \uparrow , ER stress \downarrow , inflammation \downarrow	Zhang et al. (2021)
<i>Seriola dumerili</i> , greater amberjack	Regular diet	0.3 \rightarrow 1.1	Broodstock fecundity \uparrow	Sarih et al. (2019)	
<i>S. (dorsalis) lalandi</i> , California yellowtail, broodstock		0.3 \rightarrow 2.7	Yolk sac volume \uparrow , larval survival \uparrow	Salze et al. (2019)	
<i>Sparus aurata</i> , gilthead seabream	Via <i>Brachionus rotundiformis</i> and <i>Artemia nauplii</i>	0.17 \rightarrow 6.2	WG \uparrow , vision \uparrow , hunting success \uparrow	Gaon et al. (2020)	
<i>Takifugu rubripes</i> , tiger puffer	Regular diet @ low temperature	0 \rightarrow 0.17	WG \uparrow , immunity \uparrow , apoptosis \downarrow (Fig. 11.5), oxid. Stress \downarrow	Cheng et al. (2018)	
	Low FM diet	0.6, 1.2	Bile acid biosynthesis \uparrow , cholesterol biosynthesis \uparrow , lipogenic genes \uparrow	Xu et al. (2020)	
	FM + plant-based diet	0 \rightarrow 2.0	Met sparing	Wei et al. (2020)	
<i>Thunnus thynnus</i> , bluefin tuna	Via <i>Brachionus rotundiformis</i>	0 \rightarrow 2.0 g (10 ⁶ rotifers) ⁻¹	<i>tauT</i> \downarrow \geq 1.0 g: WG \uparrow	Betancor et al. (2019)	

\uparrow support/increase; \downarrow reduction/decrease; \leftrightarrow no apparent (adverse) effect; AOC antioxidant capacity; P protein; FM fishmeal; WG weight gain; SGR specific growth rate; FCR food conversion ratio; ER stress endoplasmic reticulum stress (\rightarrow Chap. 23); *cat* catalase; *gpx* glutathione peroxidase; *cyp7a1* cholesterol 7 α -hydroxylase; *tauT* taurine transporter

^a*cyp7a1* encodes cholesterol 7 α -hydroxylase, the key enzyme in the process of converting hepatic cholesterol to bile acid (Yokogoshi et al. 1999)

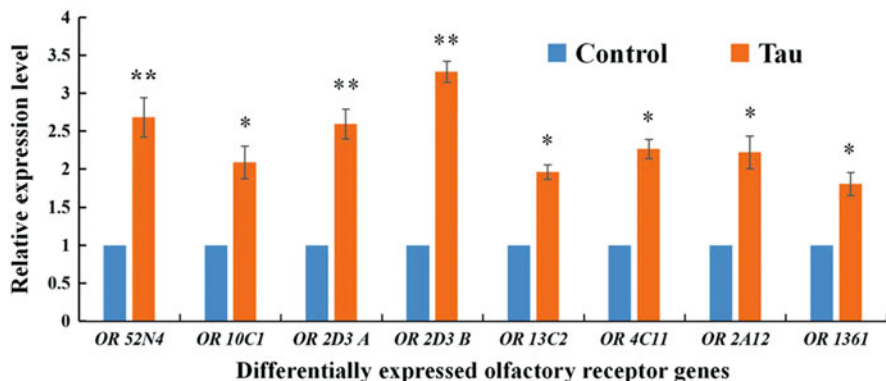


Fig. 11.4 Upregulation of eight olfactory receptor genes of large yellow croaker fed 3.5% dietary Tau. Relative expression levels were calculated according to the $2^{-\Delta\Delta CT}$ using β -actin as an internal reference gene. * $P < 0.05$ and ** $P < 0.01$. (From Hu et al. (2018), with permission from Wiley)

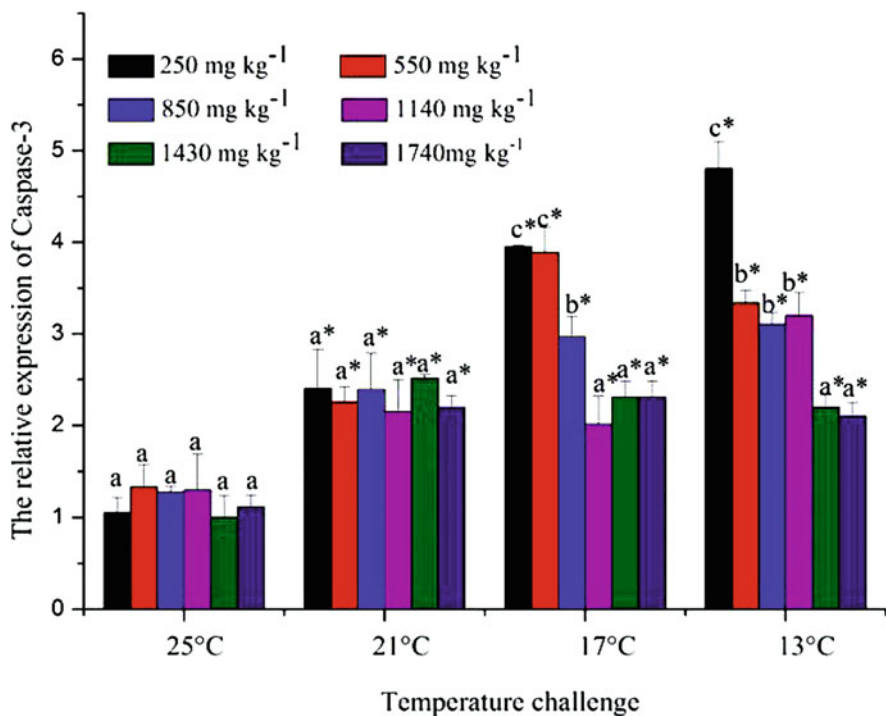


Fig. 11.5 Effects of Tau on relative expression levels of *caspase-3* under low-temperature stress in obscure pufferfish (*Takifugu obscurus*). Note: Data are expressed as mean + SD ($n = 6$). Diverse small letters show significant differences ($P < 0.05$) in different groups at the same time point in Duncan's test. (From Cheng et al. (2018), with permission from Elsevier)

exerts anti-apoptotic action by reduction of *caspase-3* transcription at low temperatures (Fig. 11.5).

The effect of dietary Tau supplementation to aquatic broodstock animals and their offspring is scarcely studied. One of the few papers shows that parental 2.7% dietary Tau increases the yolk sac volume and, thus, survival of newly hatched larvae of the California yellowtail (Salze et al. 2019).

Because Tau is that central in many physiological processes, the question arises whether animals can decide to feed on Tau-rich diets if they have the choice. Angell et al. (2012) offered this choice to ass’s-ear abalone (*Haliotis asinina*) in the form of eight species of brown, red, and green macroalgae varying in nutrient composition. The abalone consistently prefers *Hypnea pannosa* (red alga) and *Ulva flexuosa* (green alga). *H. pannosa* is rich in Tau, but *U. flexuosa* lacks this AA. Furthermore, the richest alga in Tau is *Jania crassa* (red alga) which is less preferred by *H. asinina* than the Tau-free *U. flexuosa*. This shows that no direct link exists between algal Tau content and the preference of *H. asinina*.

Similarly in planktonic freshwater cladocerans: in feeding experiments with three different coccal green freshwater algae, differing in Tau contents, it occurs that the Tau content does not steer life history traits in *Daphnia magna*, *Moina macrocopa*, and *M. micrura* (Bouchnak and Steinberg 2013, 2014). Instead, the contents of the AAs, Arg and His, influence the life span of *Daphnia*, whereas the traits of the *Moina* sp. appear to be independent of individual AAs.

Only a few trials are dedicated to the effects of dietary Tau on physiology and growth in shrimps. These studies indicate that penaeids (*P. monodon*, *L. vannamei*) require this AA for optimal performance during larval and grow-out stages, accelerated larval molting rates, and improved survival rates. However, excess Tau appears to be toxic to *L. vannamei* larvae (El-Sayed 2014). This statement is in good compliance with several recent fish studies showing that excess Tau has adverse effects on the development of fish larvae. Studying the survival rates of larval yellowtail kingfish (*Seriola lalandi*), Partridge and Woolley (2016) assume toxic action of Tau excess.

Also in Persian sturgeon (*Acipenser persicus*), adverse effects of dietary Tau are reported. Increased dietary Tau results in decreased feed intake and reduced growth (Hoseini et al. 2017). The authors assume that the tested Tau levels (0.25–1.6%) exceed the actual demand (Hoseini et al. 2018). Studies with lower dietary Tau levels are pending.

11.2 Taurine and Immunity

Table 11.1 includes several hints that dietary Tau increases innate immunity of aquatic animals. Comprehensive surveys of underlying mechanisms, however, are scarce. In one of their biomolecular studies in young grass carps, Yan et al. (2019) identified the multifaceted role of dietary Tau in the immune function—besides improvement of growth. Dietary Tau

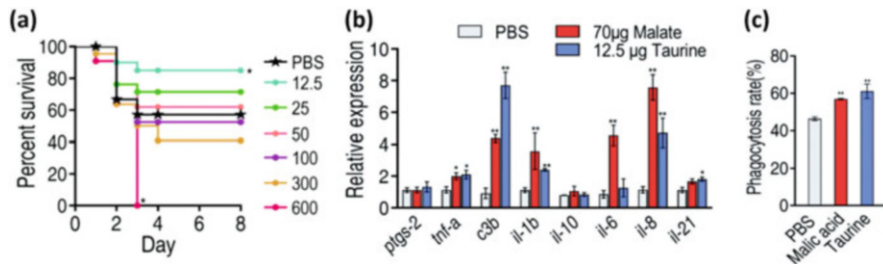


Fig. 11.6 (a) Survival of zebrafish in the presence of graded doses of Tau (in μg), 21 zebrafish each group. (b, c) Expression of innate immunity genes in zebrafish in the presence of 70 μg malate or 12.5 μg Tau (b). Twenty-five zebrafish spleens were collected in each group. Five were pooled as a sample, yielding five biological repeats for analysis of gene expression. Samples were collected in 24 h after the injection of malate or Tau for 3 days. (c) Phagocytosis in the absence or presence of 70 μg malate or 12.5 μg Tau. Macrophages were separated from the head kidney of Nile tilapia and incubated with 20 mM malate or Tau. Then, 1:100 bacterial cells were added. Three biological repeats were performed. Results are displayed as mean \pm SEM, and significant differences are identified ($*P < 0.05$, $**P < 0.01$) as determined by two-tailed Student's t-test. (From Yang et al. (2020), credit Taylor and Francis). *ptgs-2* prostaglandin-endoperoxide synthase 2 involved in the conversion of arachidonic acid to prostaglandin H₂, an important precursor of prostacyclin, which is expressed in inflammation; *tnf- α* , tumor necrosis factor α , a pro-inflammatory cytokine; *c3b*, part of complement component 3 (\rightarrow box in Chap. 2); *il-1 β* pro-inflammatory interleukin 1 β ; *il-10* anti-inflammatory interleukin 10; *il-6* interleukin 6 pro-inflammatory cytokine and anti-inflammatory myokine; *il-8* pro-inflammatory interleukin 8; *il-21* interleukin 21 induces cell division/proliferation; *PBS* phosphate-buffered saline. Inflammation follows a biphasic stage starting with initiation, where cells are attracted toward the affected side and release pro-inflammatory signal molecules and ROS (Kany et al. 2019). In the resolving phase, anti-inflammatory molecules are released to end the inflammation (Opal and DePaolo 2000).

- (a) Strengthens the ability against enteritis.
- (b) Increases antimicrobial compounds.
- (c) Downregulates pro-inflammatory cytokines and upregulates anti-inflammatory cytokines.

In zebrafish, dietary malate triggered a metabolic shift via activating the TCA cycle, leading to elevated Tau production (Yang et al. 2020). To prove the efficiency of Tau, this AA is supplemented. In fact, exogenous Tau increases the survival of zebrafish after *Vibrio alginolyticus* infection (Fig. 11.6a) as malate did as well. Moreover, exogenous Tau and malate regulate the transcription of innate immunity genes (Fig. 11.6b), boost phagocytosis (Fig. 11.6c), and promote the generation of ROS and activated nitrogen oxide. The two metabolites alleviate excessive immune responses to bacterial challenge and protect from bacterial infection. Reprogramming the metabolome with exogenous Tau is also beneficially effective in crucian carp, reared at elevated temperatures (Jiang et al. 2019) (\rightarrow Chap. 26).

11.3 Interactions with Nutrients

An intensive interplay exists between Tau and other AAs, not only with the S-containing AAs. Recently, Candebat et al. (2020) showed that adequate dietary Met spares dietary Tau; and vice versa, insufficient dietary Met induces increased Tau demand in juvenile yellowtail kingfish (*Seriola lalandi*).

In larval Nile tilapia, a number of AAs (Trp, Arg, His, Leu, Ile, Val, Ala, Gly, Thr, and Tau) increase with increasing supplemental Tau up to 10 g kg⁻¹. However, with further Tau increase, body AAs decrease (Al-Feky et al. 2015). This indicates that excessive Tau is excreted to keep body Tau at optimal concentrations. This process is energy demanding and therefore reduced growth occurs. This phenomenon is documented in juvenile Pacific white shrimp (Yue et al. 2013), rainbow trout, and gilthead seabream (Al-Feky et al. 2015). At the first glance, the above explanation seems plausible; however, it is unlikely that the pure excretion without any transformation is that energy demanding that growth retardation results (Steinberg 2012). Therefore, an additional or even alternate mechanistic background for the adverse effect must apply. Excessive dietary Tau can also lead to cessation of growth rates through reducing feed intake, as shown in Japanese flounder (Park et al. 2002) or rainbow trout (Gaylord et al. 2006). Furthermore, Glover and Hogstrand (2002) showed that Tau increases subepithelial zinc accumulation in rainbow trout but decreases the passage of zinc to post-intestinal compartments. Since zinc is both a nutrient and a toxicant of importance and since Tau is the most abundant free AA in intestinal mucosa of fishes (Auerswald et al. 1997), this may be an alternate toxicity mode of action of excess Tau.

11.4 Concluding Remark

Tau can be considered essential to most aquatic animals. However, many details of its metabolism of dietary normal and excess doses have been identified only phenotypically. Dietary excess Tau deserves special attention. Details remain to be proven and abstracted from individual levels by innovative biomolecular approaches. Here, innovative approaches means application of omics techniques not only as sophisticated monitoring tools, for instance, some transcription of genes as weak hint of the underlying pathway; rather, it means to apply these techniques so comprehensive that signaling pathways can be proposed. Furthermore, the role of the intestine microbiota in Tau metabolism has not yet been considered. Combining next-generation sequencing with proteomics or metabolomics will possibly identify comprehensive signaling pathways for growth or reproduction. Moreover, beneficial effects have to be observed if, or how, they translate into succeeding generations.

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