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Dietary Taurine Alters Behavioral Responses to an Olfactory Stimulus in Sablefish (*Anoplopoma fimbria*)

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Dietary Taurine Alters Behavioral Responses to an Olfactory Stimulus in Sablefish (*Anoplopoma fimbria*)

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Background

Sablefish, also known as black cod, is a deepwater species found in the northeastern Pacific Ocean. A delicious, high-protein source of omega-3 fatty acids, sablefish are also a potential species for commercial farming. Here at NWFSC, we are experimenting with raising them in order to better understand their needs—one of which is taurine. Taurine is a newly identified, essential dietary nutrient for many marine fish species. Including taurine in aquafeeds improves fish growth and feed performance, and may improve their ability to smell.

We conducted a behavioral experiment to measure how juvenile sablefish respond to a food odor, to find out if there was a difference between fish that were fed a low-taurine, plant-based diet versus those given an otherwise identical feed supplemented with 1% taurine.

Key Takeaways

Fish fed the taurine-supplemented feed had higher whole-body taurine levels than fish fed the unsupplemented feed. In addition, the fish that ate the taurine-supplemented aquafeed had a stronger response to the introduction of a food odor into their tank.

Taurine levels in aquaculture feeds should be of concern to growers, as not enough taurine may have negative effects beyond just growth. This study suggests that too little dietary taurine may affect a fish's ability to smell, which may worsen their feeding response, reproduction, and other behaviors.

Links used in this section:

- Sablefish: https://www.fisheries.noaa.gov/species/sablefish
- Commercial farming: https://www.fisheries.noaa.gov/west-coast/aquaculture/aquaculture-science-and-research-west-coast
- We are experimenting with raising them: https://www.fisheries.noaa.gov/west-coast/aquaculture/sablefish-aquaculture-pacific-northwest
- Taurine: https://www.fisheries.noaa.gov/feature-story/nwfsc-wins-aafco-approval-taurine-fish-feeds
- Aquafeeds: https://www.fisheries.noaa.gov/feature-story/5-things-know-about-aquafeeds

Abstract

Though relatively high concentrations of taurine are found in the olfactory bulb, the part of the brain that receives messages from the olfactory epithelium, few studies have explored the role that taurine plays in olfactory function, which is important for triggering feeding behavior, food consumption, and ultimately growth. A behavioral experiment was conducted to measure the response of juvenile sablefish to a food odor to determine whether there was a difference between fish fed a low-taurine, plant-based diet versus those fed an otherwise identical diet supplemented with 1% taurine. Fish fed the taurine-supplemented feed (1 TAU) had a significantly higher whole-body taurine concentration, 0.208 ± 0.029% than fish fed the unsupplemented feed (0 TAU), 0.069 ± 0.010%, $p < 0.0001$. The initiation of a search response by the introduction of a food odor was stronger in fish fed the taurine supplemented diet: 0 TAU $n = 58$, 1 TAU $n = 59$, $p = 0.001$. Taurine levels in feed should be of concern to growers, as a lack of taurine may have effects beyond just growth. This study suggests that a lack of dietary taurine may affect olfactory function, which may negatively impact feeding response, reproduction, or other olfactory-mediated behaviors.

Acknowledgments

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Data availability

Data are available upon request. To request data, please contact Ronald B. Johnson, ronald.b.johnson@noaa.gov.

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1 Introduction

The development of alternative aquaculture feeds that are both environmentally sustainable and commercially viable is an important topic in aquaculture and essential to supporting sustainable marine aquaculture goals (FAO 2022). To accomplish this, feeds are being developed that replace traditional marine fish ingredients with terrestrial alternatives (Rust et al. 2011, Hua et al. 2019, FAO 2022).

Although plant-derived proteins are commonly used in aquaculture feeds, the complete replacement of fishmeal by plant proteins is problematic due to nutritional deficiencies, palatability issues, and anti-nutritional factors such as protease inhibitors found in soybeans. One of these nutritional deficiencies for marine fish is taurine. Taurine is a sulfonic acid and is naturally abundant as a free acid in animal meals, but present in only limited quantities in terrestrial plants (Salze and Davis 2015). Some fish can biosynthesize taurine when dietary taurine is absent, but this has been shown to be limited in carnivorous fish (Takagi et al. 2011, Salze and Davis 2015, Sampath et al. 2020). In previous work, decreased feed intake and reduced fish growth were observed in marine fish fed plant-based diets not supplemented with taurine (Johnson et al. 2015, Sampath et al. 2020). While the relationship between a low taurine diet and reduced growth and feed intake is generally recognized for many species, the reason for this relationship is not well understood (Martinez et al. 2004, Kim et al. 2017, Hu et al. 2018, Adeshina and Abdel-Tawwab 2020, Li et al. 2022, Senzui and Fukada 2022).

Taurine plays an important role in many physiological processes and is abundant in the brain, retina, and throughout the body (Oja and Saransaari 2007, Ripps and Shen 2012). It is thought to be a cytoprotectant and supports cell membrane integrity and osmotic balance (Oja and Saransaari 2007, El-Sayed 2013). Taurine deficiency is associated with impaired retinal development and pathologies of the heart, kidney, and pancreas (Ripps and Shen 2012, Salze and Davis 2015). Taurine also appears to perform many of the functions of a neurotransmitter and may act as an inhibitory neurotransmitter, though the specific mechanisms are not well known (Chaput et al. 2004, Wu and Prentice 2010, Ripps and Shen 2012). Relatively high concentrations of taurine are found in the olfactory bulb, the part of the brain that receives messages from the olfactory epithelia (Chaput et al. 2004, Saransaari and Oja 2008). While there is some evidence that taurine functions as a feed stimulant, and ample evidence that low levels of dietary taurine are associated with reduced growth, few studies exist that demonstrate the role that taurine plays in olfactory function (Martinez et al. 2004). Studies have demonstrated that taurine can regulate the conductance of Cl^-, K^+, and nonselective cations in certain olfactory receptor neurons in the mudpuppy and olfactory bulb tissue in rats (Dubin and Dionne 1993, Belluzzi et al. 2004). Taurine is also thought to work with GABA receptors in the olfactory bulb to inhibit the spontaneous firing of neurons, reducing random background firing of neurons and effectively increasing the signal-to-noise ratio for stimulatory-induced neural signals (Belluzzi et al. 2004, Chaput et al. 2004). Given the role that taurine has been shown to play in neural function and the high concentrations of taurine in the olfactory bulb, it seems likely that taurine may play a role in olfactory function and that a taurine deficiency could negatively impact not only olfactory function but olfactory-dependent behaviors.

This study was designed to explore whether juvenile sablefish fed a diet deficient in taurine have a reduced olfactory response by evaluating changes in behavioral response to a food odor. A behavioral analysis method was used to measure the response of juvenile sablefish to a food odor to determine whether there was a difference between fish fed alternative (plant-based) diets without added taurine versus those fed an otherwise identical diet supplemented with 1% taurine.

2 Materials and Methods

2.1 Fish and Feeding

In 2017, female sablefish raised at the Northwest Fisheries Science Center's Manchester Research Station (Manchester, Washington) were transported to an indoor saltwater recirculation system at NWFSC (Seattle, Washington). Initial length and weight measurements and passive integrated transponder (PIT) tagging were completed on 9 March 2017. All fish were individually PIT-tagged (Biomark, Boise, Idaho), and ranged in weight from 55.5 g to 123.5 g and in length from 109 mm to 249 mm fork length (FL). Prior to the start of the experiment, fish were fed a commercial salmon diet to apparent satiation three times per week (Biobrood; BioOregon, Longview, Washington).

On 6 April 2017, 72 hours post-feeding, fish were transferred to NWFSC's Mukilteo Field Station (Mukilteo, Washington) and placed on a flow-through, sand-filtered seawater system (salinity 30%, pH 7.8, oxygen 9.5 mg/L, temperature 10–12°C). Fish were anesthetized and individually measured for length and weight. Fish were then split evenly between two tanks (diameter 2 m)—one randomly selected fish at a time was added to either the "no taurine" or "1% taurine" tank—and the feeding of the experimental diets began. Fish were held at ambient photoperiod and temperature; weights ranged from 56.1 g to 142.1 g, and lengths ranged from 185 mm to 260 mm FL.

The two experimental groups of sablefish in this study were both fed an alternative, plant-based diet. One group (1 TAU) of 59 fish was fed a diet supplemented with 1% taurine. The other group (0 TAU) of 58 fish was fed a diet without taurine added. The experimental feeds contained an average of 48.0% crude protein and an average of 7.8% crude lipid, with soy protein concentrate and corn protein concentrate as the primary sources of protein (Table 1). Previous studies have verified that taurine is absent from these ingredients (Johnson et al. 2015). Fish meal was a minor ingredient that introduced a small amount of taurine to the unsupplemented (0 TAU) feed. The taurine-supplemented (1 TAU) feed included 1% added taurine. All the dietary ingredients were pulverized and mixed. Extruded pellets were produced by twin-screw extruder (ATX-II; Fesco, Daegu, Korea) equipped with a 4 mm die. Fish were sampled between 13 October 2017 and 14 June 2018, after 190–434 days on experimental feed. Initially, fish were fed approximately 2% body weight per day, three days per week, via an automatic feeder. During the behavior trials, fish were fed a small amount of food in the morning. This was found to increase their responsiveness to a food odor. At the end of the day, fish were fed to excess.

2.2 Behavioral Research Methods

The methods used were similar to those used previously to detect avoidance of a test substance (Sommers et al. 2016). Briefly, the chamber consisted of a 1.8 m diameter, 74 cm tall circular fiberglass tank, 35 cm depth, divided into six segments with a central distribution manifold (Figure 1). Water flowed from a central manifold to drains spaced around the wall of the tank at the center of each segment. Flow entered at the head of each segment at the bottom. Flow was also directed along the edge of each segment, where sheets of twin-wall polycarbonate created a laminar flow effect to help isolate water between segments while allowing fish to swim freely around the tank. The test substance was pumped into the distribution chamber of the exposure segment (Segment 1) so that it mixed with water flowing into the bottom center at the head of the experimental portion of the exposed segment. Dye tests verified that the incoming water was contained within the exposure segment. Total flow into the tank was 45 Lpm (12 gpm). Total tank volume was ~890 L (233 gal).

Table 1. Ingredients and proximate composition of experimental diets.

	Concentration (%)	
Ingredient	**0 TAU**	**1 TAU**
Soy protein concentrate[a]	25.30	24.80
Corn protein concentrate	21.90	21.50
Wheat flour	28.50	28.40
Fish meal	9.00	9.00
Fish oil	8.50	8.50
Fish gelatin (cod)[b]	2.00	2.00
Mineral premix[c]	0.10	0.10
Vitamin premix[d]	1.50	1.50
Vitamin C[e]	0.10	0.10
Choline[f]	0.50	0.50
Betaine[g]	0.25	0.25
L-methionine	0.16	0.16
L-lysine	0.20	0.20
Dicalcium phosphate	2.00	2.00
Taurine		1.00
Proximate composition analyzed (Dry matter, %)		
Crude protein	47.6	48.4
Crude lipid	8.4	7.4
Ash	6.3	6.4
Moisture	6.7	6.7

[a] Profine-S, Milae Resources M L Co. Ltd., Seoul, Korea.
[b] Jellybond, Dabol Co. Ltd., Gyeonggi-do, Korea.
[c] Mineral premix contained the following ingredients (g/kg premix): NaCl, 43.3; $MgSO_4 \cdot 7H_2O$, 136.5; $NaH_2PO_4 \cdot 2H_2O$, 86.9; KH_2PO_4, 239; $CaHPO_4$, 135.3; Ferric citrate, 29.6; $ZnSO_4 \cdot 7H_2O$, 21.9; Ca-lactate, 304; CuCl, 0.2; $AlCl_3 \cdot 6H_2O$, 0.15; KI, 0.15; $MnSO_4 \cdot H_2O$, 2.0; $CoCl_2 \cdot 6H_2O$, 1.0.
[d] Vitamin premix contained the following amounts which were diluted in cellulose (g/kg premix): L-ascorbic acid, 121.2; DL-α-tocopheryl acetate, 18.8; thiamin hydrochloride, 2.7; riboflavin, 9.1; pyridoxine hydrochloride, 1.8; niacin, 36.4; Ca-D-pantothenate, 12.7; myo-inositol, 181.8; D-biotin, 0.27; folic acid, 0.68; p-aminobenzoic acid, 18.2; menadione, 1.8; retinyl acetate, 0.73; cholecalciferol, 0.003.
[e] Stay-C (50%), DSM Nutritional Products Canada Inc., Parsippany NJ, Canada.
[f] Choline chloride (50%), Solton Biochem Co., Cheonan, Korea.
[g] CTCBIO Co. Ltd., Gyeonggi-do, Korea.

An attractive odor solution for behavior trials was generated by soaking 150 g of thawed, chopped squid mantle (Del Mar Seafoods Inc., Watsonville, California) in 2 L of seawater for two hours and then straining out the mantle material. The extract was prepared the day of each trial and kept at ambient seawater temperature (~10°C) in a water bath for the duration of the day (~5 hours). This odorant is similar to methods used in a variety of other behavioral studies (Davis et al. 2006). Trials consisted of a single fish being placed in the behavioral chamber and allowed to acclimatize for 1 hour. Feeding schedules were established to provide the most reliable response to the squid extract. A 24-hour fast prior to a behavior trial was found to produce the best response, with feeding a small amount of feed the morning of the trial.

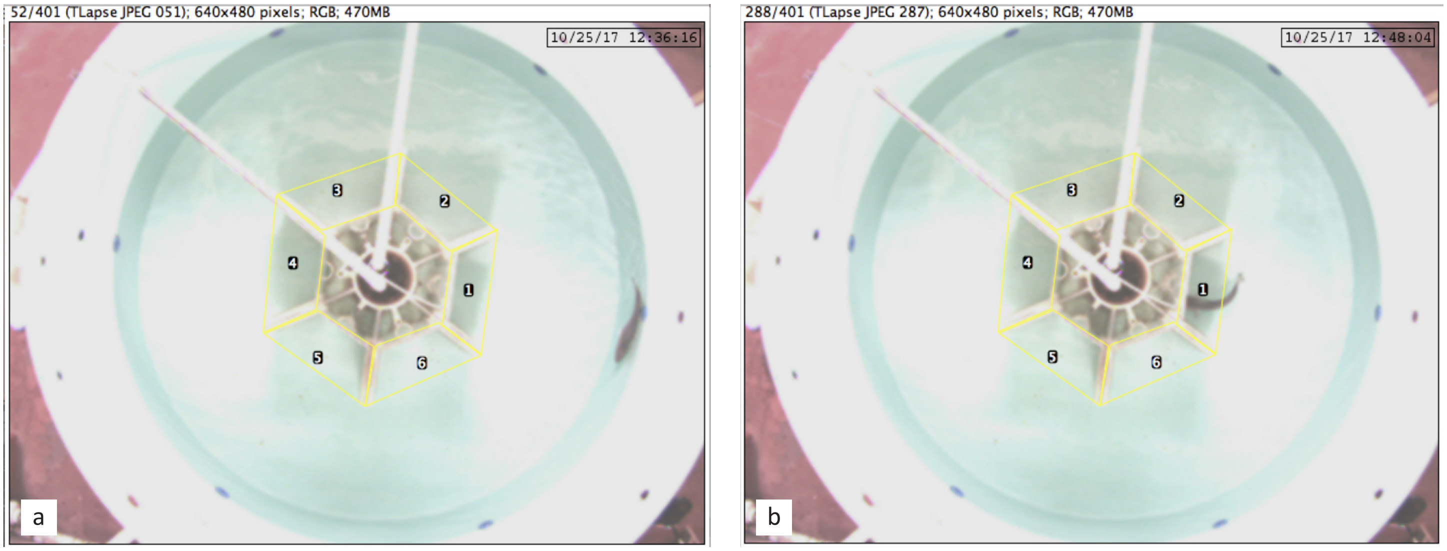

Figure 1. Images showing a fish during the behavior trial and the placement of ROIs. Figure 1a shows a fish outside the ROIs, and Figure 1b shows one inside.

At the initiation of a trial, a firewire camera (DFK 21F04; Unibrain Inc., San Ramon, California) mounted above the tank began capturing still images of fish position at three-second intervals using time-lapse software (BTV Pro; Ben Software, London, United Kingdom). At the initiation of each trial, the intake for the metering pump would be set to pump ambient seawater at 25 mL/min into the exposure segment. At ten minutes into the trial, the intake to the metering pump was switched to the test odorant and continued for ten more minutes. Each individual trial produced a folder with 400 images, 200 where ambient seawater is being pumped into the exposure segment and 200 where the odorant is being pumped into the exposure segment. After the end of each trial, the pump intake was switched back to seawater and the tank was allowed to clear for one hour before a new fish was placed in the tank. One hour was sufficient to clear the odorant from the tank between trials, based on dye tests and observation of fish behavior. The order in which treatment fish were tested was alternated between subsequent days so that if the first fish tested was a high-taurine fish, the next day the first fish would be from the low-taurine treatment. Each day, treatments tested were alternated from one run to the next.

2.3 Data Collection and Analysis

Behavioral responses were scored by identifying a measurable behavior that indicated a response to the odorant. From initial trials it was observed that without squid extract present, fish tended to swim in circles around the periphery of the tank. With the squid extract present, fish changed behavior and spent more time closer to the center of the tank. Using this observation, Regions of Interest (ROIs) were established around the central manifold of the tank, not extending past the manifold "fins" (Figure 1) and combined into one "central ROI." Image analysis software was used to score fish position in the tank. Presence of the fish in the central ROI was then compared between pre- and post-exposure recordings.

Images were processed with ImageJ software (NIH, Bethesda, Maryland; Schneider et al. 2012). For each fish, this resulted in a value (1 or 0) for each of the 200 images before the odorant was present where ambient seawater is being pumped into the exposure segment and the

200 images where the odorant is being pumped into the exposure segment. In each of these images, the fish was either in (1) or not in (0) the ROI. Percentages of images with the fish in the ROI were then arcsin transformed and compared between pre- and post-exposure recordings by Students t-test using StatView statistical software (Abacus Concepts, Inc. Berkeley, California).

2.4 Whole-Body Taurine Analysis

After each run, fish were anesthetized with MS-222 followed by cervical dislocation, and frozen. Twenty fish were selected at random from each treatment group for whole-body taurine analysis. Fish were ground and freeze-dried, then submitted to the University of Missouri Experimental Station Chemical Laboratories (Columbia, Missouri) for taurine content in accordance with AOAC Official Method 982.30 (AOAC 2000). Whole-body taurine content on a wet weight basis was compared between groups by unpaired Student's t-test using StatView statistical software (Abacus Concepts, Inc.).

3 Results

3.1 Response to an Odorant

There was no significant difference between groups of fish spending time in the ROI when no odorant was present (Figure 2): 0 TAU $n = 58$, 1 TAU $n = 59$, $p = 0.1987$. This demonstrates that neither treatment group displayed a preference for the center ROI of the tank prior to the introduction of the squid extract. Without squid extract present, 0 TAU and 1 TAU fish spent an average of 0.32% and 0.57% of their time in the center ROI, respectively.

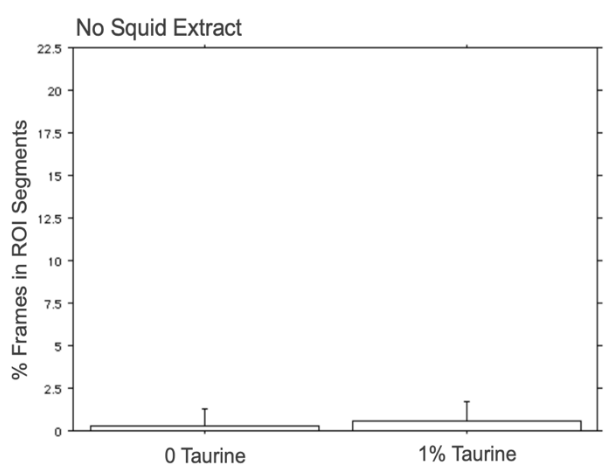

Figure 2. Percentage of frames where a fish was present within the ROI segment when no squid extract was present. 0 TAU $n = 58$, 1 TAU $n = 59$, $p = 0.1987$. The bar graph represents the mean and the error bars the standard deviation (SD).

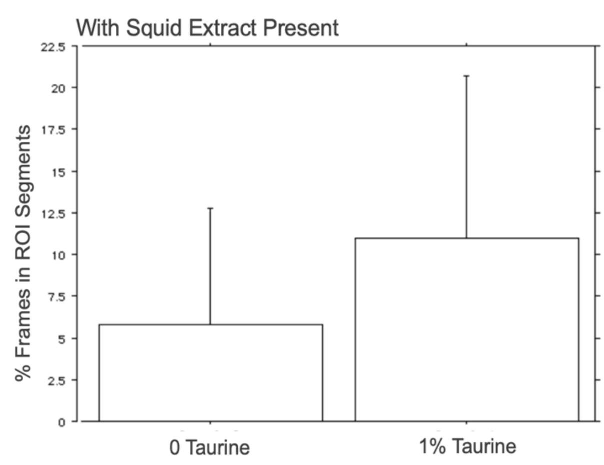

Figure 3. Percentage of frames where a fish was present within the ROI segment when squid extract was present. 0 TAU $n = 58$, 1 TAU $n = 59$, $p = 0.0011$. The bar graph represents the mean and the error bars the standard deviation (SD).

In the presence of the squid extract, fish from both groups spent more time in the central ROI. Fish that received the experimental feed with 1% taurine were more likely to be in the exposure segment than fish that received the unsupplemented feed, with 0 TAU fish spending 5.8% of their time in the central ROI and 1 TAU fish spending 11.0% (Figure 3; 0 TAU $n = 58$, 1 TAU $n = 59$, $p = 0.0011$).

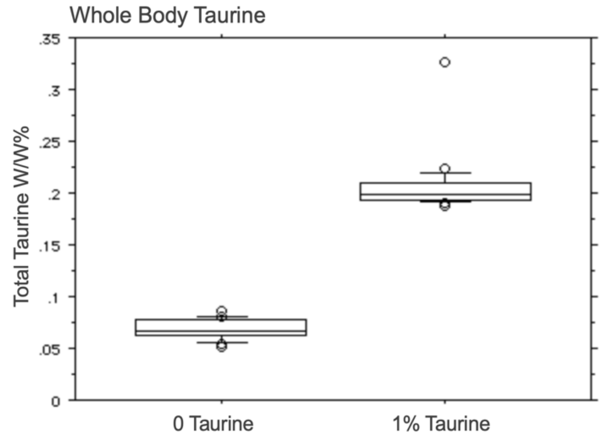

Figure 4. Box plot showing whole body taurine wet weight percentage for low-taurine (0 TAU) and 1% added taurine (1 TAU) diets; $n = 20$, $p > 0.0001$.

3.2 Whole-Body Taurine

The fish that received the experimental feed with added taurine had significantly higher whole-body levels of taurine (Figure 4; $n = 20$ per treatment, $p \leq 0.0001$). On average, fish fed the unsupplemented diet (0 TAU) contained 0.069 ± 0.010% taurine on a wet weight basis. In contrast, fish fed the taurine-supplemented diet (1 TAU) contained an average of 0.208 ± 0.029% taurine.

4 Discussion

The search response initiated by the introduction of a food odor was stronger in fish fed a taurine level found to support optimal growth than in fish receiving a diet that was low in taurine. Behavior was clearly altered when squid extract was introduced into the chamber. Increased presence in the central ROI of the behavior chamber in response to the introduction of squid extract was different between fish that received feed supplemented with taurine and those that received the unsupplemented feed. Since the initiation of the search response, in this case, was driven by olfaction, one possible explanation for the difference between the two study groups is a difference in olfactory function.

As previously stated, olfactory function plays an important role in initiating a feed response (Valentinčič and Caprio 1997, Hara 2006). Taurine appears to play an important role in olfactory function given its high concentration in the olfactory bulb, and appears to mediate neuron function in the bulb. Whole-body taurine levels of 0 TAU fish in this study are significantly lower than those of 1 TAU fish, and similar to those from fish showing sub-optimal growth in a previous study (Johnson et al. 2015).

Previous studies have demonstrated the need for adequate dietary taurine for growth and feed intake for a wide variety of fish species, including sablefish (Johnson et al. 2015, Salze and Davis 2015, Kim et al. 2017, Adeshina and Abdel-Tawwab 2020, Sampath et al. 2020, Li et al. 2022). This study attempts to isolate taurine-dependent olfactory function by quantifying the search response to an identical stimulant for both experimental feed groups.

Taurine levels in fish feeds should be of concern to growers, as lack of taurine may have adverse effects beyond growth. This study demonstrates the possible impact that a lack of dietary taurine can have on olfactory function, which could affect growth, reproduction and spawning, or other olfactory-mediated behaviors. Ensuring aquaculture feeds contain sufficient amounts of taurine for optimal olfaction may promote an enhanced feeding response, which would likely result in better growth performance, as well as other factors that may improve overall fish health.

5 Conclusions

Taurine deficiency appears to adversely affect olfactory function in sablefish. Relatively low whole-body taurine levels occur in sablefish fed a low-taurine, plant-based diet. Sablefish fed a low dietary taurine diet had a reduced behavioral response to food odor.

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