Research Article

Effect of Dietary Carbohydrate Forms on Zootechnical Parameters and Liver Histology of the Malaysian Mahseer, *Tor tambroides*

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Abstract | Carbohydrates play a crucial role in the natural diet of freshwater fish by serving as a readily available energy source that support metabolic functions and spares protein for growth and tissue repair. Their utilization efficiency varies among species, influenced by digestive physiology, feeding habits, and the complexity of carbohydrate types present in the natural environment. Despite growing interest in carbohydrate utilization in tropical freshwater species, there is limited information on the ability of Malaysian mahseer *T. tambroides* to utilize simple sugars compared to complex polysaccharides. This study evaluates two simple forms of carbohydrates in the diets of *T. tambroides* against starch. In an eight-week feeding trial, soluble polysaccharide (starch) was incorporated at 234.4 g kg^{-1} dry matter (control diet), whereas monosaccharide (glucose) and disaccharide (sucrose) were incorporated to completely replace the starch in the diet for the treatment groups. Fish responses to these diets in terms of growth performance, feed efficiency, body composition, and liver histology were assessed. Fish fed simple sugars exhibited significantly lower protein, lipid, and energy retention values (PRV, LRV, ERV); approximately half or less of those observed in the starch-fed group. Conversely, carbohydrate retention (CRV) was notably higher in these groups, indicating an inefficient utilization of dietary glucose and sucrose by *T. tambroides*. Nonetheless, observation of liver histology did not reveal any deleterious effects of the dietary treatments. This study concludes that complex polysaccharides are better utilized than simple sugars to fulfill the dietary exogenous carbohydrate needs of *T. tambroides*.

Keywords | Glucose metabolism, Cyprinid fish, Disaccharide, Monosaccharide, Polysaccharide.

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INTRODUCTION

The cyprinid Malaysian mahseer *T. tambroides* (Bleeker, 1854), is a high-valued finfish priced at approximately USD178 kg^{-1}, with Malaysia currently the top global producer (FAO 2020; DOF 2021). This species is widely popular as game fish; white meat delicacy, and as a valuable ornamental fish (Lau *et al*., 2021). The inherently slow growth of *T. tambroides* limits production, leading commercial farmers to rely on wild-caught mature individuals to offset low yields (Ng and Andin 2011; Abduh *et al*., 2021). Since *T. tambroides* is an omnivore, its natural diet consists of smaller animals, molluscs, aquatic insects, and riverine fruits consumed for its high carbohydrate and lipid content (Tan 1980; Ambak and Jalal 2006). Boosting aquaculture production of this species through appropriate nutritional studies targeted at improving growth can reduce the tendency of wild fishing and mitigate the pressure on wild stock population.

Carbohydrates are intentionally included in aquaculture feeds to enhance pellet integrity, reduce nutrient leaching, and improve digestibility, ultimately supporting efficient nutrient uptake and farm profitability by serving as a cost-effective energy source (Sørensen 2012; Wu *et al*., 2021; Ren *et al*., 2021; Mohamed Nafees *et al*., 2022). While teleosts can utilize various carbohydrate forms, their capacity depends on species, developmental stage, size, and carbohydrate type (Zhou *et al*., 2022). Limitations in carbohydrate utilization are often linked to feeding behavior, digestive enzyme activity, and genetic variation among species (Shiau 1997; Stone 2010; NRC 2011; Adjoumani *et al*., 2022). Carnivorous and piscivorous species generally have low digestive carbohydrate activity levels, restricting their ability to digest complex carbohydrates efficiently, unlike herbivorous or omnivorous fish (Hidalgo *et al*., 1999; Chan *et al*., 2004; Jun-Sheng *et al*., 2006; Debnath *et al*., 2007; Kamalam *et al*., 2017; Corrêia *et al*., 2019). These species may benefit more from simple carbohydrates, such as monosaccharides, due to their higher digestibility and rapid absorption (Stone *et al*., 2003; Enes *et al*., 2008). However, starch supplementation has been shown to support growth in carnivorous aquaculture species like Atlantic salmon, *Salmo salar* (Hemre *et al*., 2002), European sea bass, *Dicentrarchus labrax* (Enes *et al*., 2011), cobia, *Rachycentron canadum* (Cui *et al*., 2010), hybrid striped bass, *Morone chrysops*×*M. saxatilis* (Rawles *et al*., 2008) and white sturgeon, *Acipenser transmontanus* (Deng *et al*., 2005).

Previous nutritional studies have elucidated the dietary requirements of *T. tambroides*, for boosting growth during rearing. The dietary protein requirement of the fish has been determined to be between 40% to 48% based on its different life stages (Ng *et al*., 2008; Misieng *et al*., 2011). Its dietary lipid requirement is reported to be 5% minimum (Ramezani-Fard *et al*., 2012). Meanwhile, this species possesses all required enzymes for in vivo fatty acid synthesis namely fatty acyl desaturase (Fads2) and two elongases (Elovl5, Elovl2); indicating fully functional capacity for the fish to convert C18 linoleic and linolenic acids to eicosapentaenoic acid, docosahexaenoic acid, and arachidonic acid (Sam *et al*., 2021). Ishak *et al*. (2016) had also established the optimal dietary carbohydrate of *T. tambroides* to be 23.44% while the species was demonstrated to have limited ability to utilize complex starch from different crop sources in another study by Ishak *et al*. (2021). Carbohydrate utilization could be species-specific and carbohydrate complexity might be a factor in fish physiological changes. Despite growing interest in carbohydrate nutrition and utilization in tropical freshwater fish species, there remains limited information regarding the capacity of *T. tambroides* to efficiently utilize different carbohydrate sources. In particular, comparative data on the utilization of simple sugars (such as monosaccharides and disaccharides) versus complex polysaccharides is notably scarce for this commercially important species.

In this study, we investigate the effects of different dietary carbohydrate complexities (starch, glucose, and sucrose) on growth performance, efficiency of feed utilization, body nutrient composition, and liver histology of *T. tambroides*. These are relevant in understanding the outcomes of carbohydrate complexities in *T. tambroides* diet which can then be applied in rearing other related fish species in captivity.

MATERIALS AND METHODS

Experimental flowchart

A summary of step-by-step work flow for the experiment is presented in Figure 1 followed by a detailed explanation of every step carried out during the experiment.

Preparation of experimental diets

Three diets were prepared to include carbohydrate forms of different complexities. Monosaccharides (D-glucose), disaccharides (sucrose) and soluble polysaccharides (corn starch) were purchased from Sigma-Aldrich (Merck, USA) and the feed formulations were computed through the WinFeed Least Cost Feed Formulation Software 2.8.4 (Cambridge, UK). D-glucose and sucrose were incorporated into the experimental diets for *T. tambroides* as the primary carbohydrate sources. A basal inclusion level of 50.0 g kg^{-1} corn starch was retained in all diets to facilitate diet formulation and maintain a constant total dietary carbohydrate level of 234.4 g kg^{-1}. This carbohydrate level was based on the optimal dietary

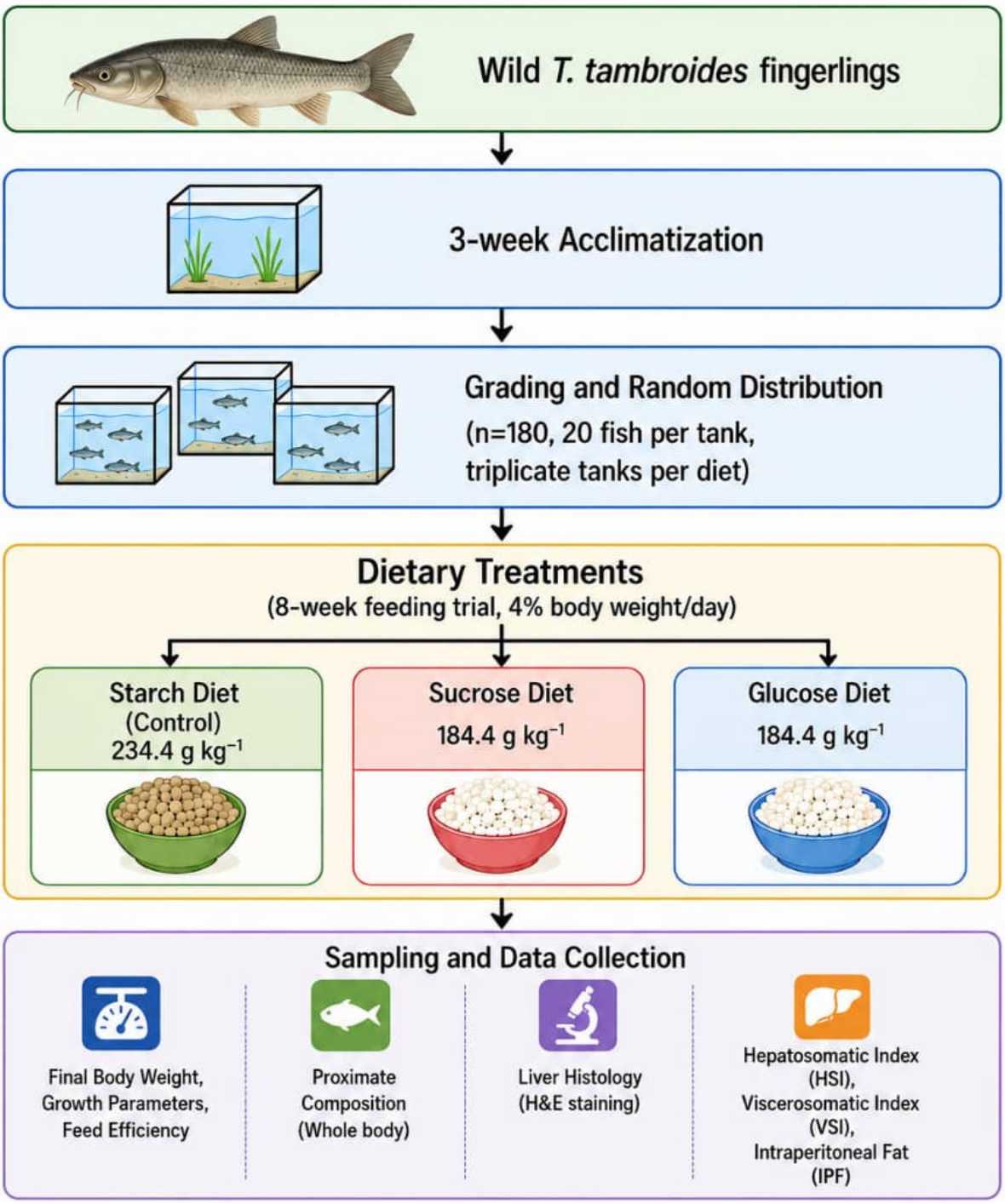

Figure 1: Flowchart of the experimental design.

requirement previously determined for *T. tambroides* by Ishak *et al*., (2016), as shown in Table 1. Local fish meal (NutriVet Trading, Malaysia) was used as the protein source, and a vegetable oil mixture of canola and sunflower oils was used as lipid source (Naturel™, Malaysia). All ingredients were then blended until homogenous by KitchenAid Countertop Stand Mixers (KitchenAid, USA) for 20 minutes. Mixtures were then conditioned to 40% wet basis content and sealed in Ziploc bags to allow moisture equilibration for 24 hours at room temperature. All diets were extruded using Brabender KE19 single-screw extruder (Brabender Gmbh and Co., Germany). For verification, the composition of glucose and sucrose in the tested diets were determined using high-performance liquid chromatography with separation performed by Varian 385-LC ELSD (Agilent Technologies), also shown in Table 1. Dilution of samples was done with acetonitrile:water (1:1 ratio) prior to chromatographic separation, before subjected to centrifugation and filtration using a nylon syringe filter, 0.45 µm. Filtered samples were next injected into a Prevail Carbohydrate ES 250 mm × 4.6 mm, 5 µm column (Alltech, USA). The mobile phase

was acetonitrile: water (75:25 ratio) at 1.0 mL min^{-1} flow rate. The values of percentage area under chromatographic peaks over the total area of peaks were used to determine sugar composition.

$$\text{Carbohydrate} = 1000\text{g kg}^{-1} - (\text{moisture} + \text{protein} + \text{lipid} + \text{ash})$$

Table 1: Diet formulation, proximate and sugar composition of the experimental diets (g kg^{-1}) as-fed basis.

	Experimental diets		
	Glucose	**Sucrose**	**Starch**
Ingredients			
Fish meal	690.0	690.0	690.0
Vegetable oil	55.6	55.6	55.6
Vitamin premix †	10.0	10.0	10.0
Mineral premix ‡	10.0	10.0	10.0
Corn starch	50.0	50.00	234.4
Sucrose	0	184.4	0
Glucose	184.4	0	0
Proximate composition			
Moisture	47.7	48.1	117.2
Protein	461.0	454.6	431.0
Lipid	93.4	87.3	101.7
Ash	87.2	90.1	105.5
Fiber	13.9	12.5	18.0
Carbohydrate	310.7	319.9	244.6
Gross energy (kJ g^{-1})	19.93	19.67	18.30
Sugar composition			
Glucose	114.1	0.7	1.0
Sucrose	< 0.1	113.4	1.0
Maltose	< 0.1	< 0.1	1.0

† Vitamin premix (g kg^{-1}); cellulose, 845.11; choline chloride, 75; ascorbic acid, 45; α-tocopheryl acetate (500 IU g^{-1}), 8; myoinositol, 5; niacin, 4.5; Ca-pantothenate, 3; riboflavin, 1; pyridoxine, 1; thiamine mononitrate, 0.92; retinyl acetate, 0.6; vitamin K menadione, 1.67; biotin, 0.02; folic acid, 0.09; vitamin B12, 0.001; cholecalciferol, 0.083.‡ Mineral premix (g kg^{-1}): $CaHPO_4.2H_2O$, 500; $CaCO_3$, 215; MgOH, 124; KCl, 90; NaCl, 40; $FeSO_4$ $7H_2O$, 20; $ZnSO_4.7H_2O$, 4; $MnSO_4.H_2O$, 3; $CuSO_4.5H_2O$, 3; NaF, 1; KI, 0.04; Na_2SeO_3, 0.03; $COSO_4$, 0.02.

Feeding trials and sampling

This experiment was conducted at the Department of Aquaculture Wet Laboratory, Universiti Putra Malaysia. Wild *T. tambroides* fingerlings were obtained from a localfish farm in Kelantan, Malaysia and subjected to three weeks of acclimatization. Following the acclimatization period, fish were graded to 180 individuals (initial body weight of 1.40 ± 0.01 g). Nine 60 L glass aquaria (38 cm × 75 cm × 35 cm) filled with dechlorinated municipal water were each stocked randomly with twenty fish and each unit was equipped with continuous aeration. Water parameters were maintained at 26.0±1.0 °C temperature, 5.0±0.5 mg l^{-1} dissolved oxygen and 6.8±0.2 pH; with up to 30% water changes done twice weekly. Experimental diets were fed daily to fish for eight weeks at 4% body weight. Fish mortality and body weight were monitored and recorded throughout the trial. The quantity of feed used during the trial was recorded as feed intake.

At the end of the feeding trial, fish were fasted for 24 hrs. before sampling. Final body weight for all fish was measured. Subsequently, ten fish from each replicate were selected randomly and euthanised following anesthetization of 1gL^{-1} tricaine methanesulfonate (MS222). Internal organs, including the liver, were excised and weighed. Fat from the abdominal cavity was combined with that separated from the viscera and classified as intraperitoneal fat. Liver was preserved for histological analysis, while eviscerated fish were freeze-dried for proximate composition analysis. Remaining live fish post-sampling were consolidated and maintained in a common holding tank under standard care. All procedural steps for animal laboratory use complied with the MYCODE for the Care and Use of Animals for Scientific Purposes (LKH/GP/01/2019) as outlined by the Animal Welfare Board, Department of Veterinary Services, Malaysia.

Subsequently growth parameters such as; weight gain (WG), and specific growth rate (SGR) were determined using the following equations:

$$\text{WG, \%} = 100 \times (\text{final body weight} - \text{initial body weight}) / \text{initial body weight}$$

$$\text{SGR, \%} = 100 \times (\ln \text{final body weight} - \ln \text{initial body weight}) / \text{days of feeding}$$

FCR and PER, were determined using the calculations below:

$$\text{FCR} = \text{weight of feed consumed} / \text{body weight gain}$$

$$\text{PER} = \text{body weight gain} / \text{protein intake}$$

Hepatosomatic index (HSI), viscerosomatic index (VSI) and intraperitoneal fat ratio (IPF) were calculated using the following equation:

$$\text{HSI, \%} = (\text{weight of sampled liver} / \text{total body weight}) \times 100$$

$$\text{VSI, \%} = (\text{weight of sampled viscera} / \text{total body weight}) \times 100$$

$$\text{IPF, \%} = (\text{weight of sampled fat} / \text{total body weight}) \times 100$$

Proximate composition analysis

Crude protein content was estimated via distillation using a 2400 Kjeltec Analyzer Unit (FOSS, Denmark) after 60

min sulfuric acid digestion at 100°C. Crude lipid content was estimated using a Foss Soxtec™ 8000 extraction unit (FOSS, Denmark). Estimation of crude fiber content in samples was determined by acid and alkaline digestions using Fibertec Cold and Hot Extractor Foss Tecator (FOSS, Denmark). Moisture content was measured by Infrared Moisture Determination Balance AD-4715 (AandD Company, Japan). Crude ash content was determined by high temperature combustion in furnace at 550°C for 6 hrs. Lastly, gross energy determination was performed using an Automatic Bomb Calorimeter AC 350 (LECO, USA). Major nutrient retention values (Protein retention value, PRV; Lipid retention value, LRV; Carbohydrate retention value, CRV; Energy retention value, ERV) were obtained from proximate analysis results and calculated using the equation:

$$\text{Nutrient retention value, \%} = (\text{Nutrient gain in fish} / \text{Nutrient intake in food}) \times 100$$

Histology

The extracted livers during sampling were directly fixed in Bouin's solution for 6 hrs, before keeping in 70% ethanol. Subsequently, tissues underwent sequential dehydration in graded ethanol concentrations following the standard histological method prior to paraffin wax embedment. Tissues were sectioned at 5µm, then subjected to haematoxylin and eosin staining before finally mounted in DPX following methods in Ishak *et al.* (2021). Slides were observed using AxioScope A1 microscope (Carl Zeiss MicroImaging GmbH, Germany).

Statistical analysis

Statistical analyses were performed with SPSS v20 (SPSS Inc., USA). Percentage data were arcsine-transformed before analysis. Results are presented as means of three samples ± standard error and were analyzed with one-way analysis of variance (ANOVA) after being subjected to the Shapiro-Wilk test for data normality and Levene's test for homogeneity. Tukey's Honestly Significant Difference (HSD) test was then used in determining difference when significance was detected at P<0.05.

RESULTS

After 8 weeks of feeding trial, the growth performance, body indices, and feed efficiency of *T. tambroides* fingerlings fed with differing carbohydrate forms are shown in Table 2. Different carbohydrate complexities in the diets had no effect (p=0.402) on survival was observed between treatments although 100% survival was recorded in fish fed starch. However, the growth of *T. tambroides* was significantly affected (p<0.05) with starch feeding showing better final growth (2.32g±0.14) than fish fed glucose, along with significantly lower FCR (3.60±0.17) and higher PER (0.73±0.03) compared to fish fed either of the simple carbohydrates. Also, feeding the dietary starch recorded significantly higher SGR (0.60±0.02) too compared to those fed with sucrose (0.35±0.02) and glucose (0.38±0.02).

Table 2: Growth performance and feed efficiency of *T. tambroides* fingerlings fed with different carbohydrate forms for 8 weeks (Initial body weight = 1.40 ± 0.01 g).

	Experimental diets		
	Glucose	**Sucrose**	**Starch**
Survival (%)	98.33±1.67	98.33±1.67	100.00±0.00
Final body weigh(g)	1.84±0.09^{b}	1.93±0.05^{ab}	2.32±0.14^{a}
WG (%)	33.56±1.75^{b}	37.66±2.08^{b}	65.69±1.84^{a}
SGR	0.35±0.02^{b}	0.38±0.02^{b}	0.60±0.02^{a}
FCR	6.02±0.25^{a}	5.73±0.16^{a}	3.60±0.17b
PER	0.37±0.02^{b}	0.40±0.01^{b}	0.73±0.03^{a}

Different superscripts in rows indicated statistical significance at P < 0.05. Values are presented as mean ±SEM (n=3). Experimental fish had an initial body weight of 1.40±0.01g.

Table 3 shows that the HSI value of fish fed starch and sucrose were higher than fish fed glucose diet, although there was no significant difference among glucose and sucrose treatments (p=0.004). No significant effects were observed for IPF (p=0.546) and VSI (p=0.265) between dietary treatments. Different carbohydrate complexities significantly affected (p<0.05) body composition except for the contents of ash and moisture is shown in Table 3. The highest (p<0.05) lipid content was recorded in fish fed starch at 110.3±1.3 g kg^{-1}. Protein, energy, and fiber contents for fish fed the glucose diet were significantly lower (p<0.05) than both fish fed starch and sucrose diets. In contrast, fish fed starch had the lowest body carbohydrate content (p<0.05) than other treatments. Highest PRV (11.97±0.55%, p=0.000), LRV (54.30±2.38%, p=0.000), and ERV (32.75±1.50%, p=0.000) values were obtained in fish fed with starch but its CRV value was the lowest at 0.58±0.03% (p=0.002) as compared to other treatments.

The liver cross sections of *T. tambroides* fingerlings from each treatment showed normal staining character of the hepatocytes, intact cellular and sinusoid structure with no steatosis, or any evidence of nucleus degeneration or negative differences (Figure 2). Previous histological observations showed that liver morphology of *T. tambroides* is significantly altered by difference in carbohydrate sources and inclusion levels (Ishak *et al.*, 2016; Ishak *et al.*, 2021). These dietary factors generate excess carbohydrate, which fish metabolize and then store in hepatic tissues as glycogen and lipid vacuoles (Kamalam *et al.*, 2017).

Table 3: Body indices, body proximate composition (g kg^{-1}) per fed basis and nutrient retention percentage of *T. tambroides* fingerlings fed with different carbohydrate forms for 8 weeks.

	Body composition		
	Glucose	**Sucrose**	**Starch**
Body indices			
HSI (%)	1.03±0.08^{b}	1.32±0.15^{ab}	1.66±0.12^{a}
VSI (%)	3.53±0.17	3.16±0.21	3.04±0.19
IPF (%)	0.66±0.10	0.66±0.08	0.81±0.10
Proximate composition			
Moisture	726.5±2.0	705.3±10.2	692.0±9.5
Protein	150.5±1.6^{b}	162.8±2.3^{a}	161.8±1.9^{a}
Lipid	67.9±0.8^{c}	81.8±1.2^{b}	110.3±1.3^{a}
Ash	39.8±0.5	36.1±0.7	36.7±0.9
Fiber	0.4±0.2^{b}	1.7±0.0^{ab}	3.5±1.5^{a}
Carbohydrate †	15.4±1.6^{a}	14.1±2.3^{a}	4.3±2.0^{b}
Gross energy (kJ g^{-1})	16.90±0.45^{b}	17.68±3.0^{ab}	18.70±1.3^{a}
Nutrient retention values			
PRV (%)	4.52±0.25^{c}	6.86±0.17^{b}	11.97±0.55^{a}
LRV (%)	10.42±0.57^{c}	23.34±0.39^{b}	54.30±2.38^{a}
CRV (%)	2.75±0.03^{a}	2.34±0.04^{a}	0.58±0.03^{b}
ERV (%)	10.63±0.68^{c}	14.47±0.49^{b}	32.75±1.50^{a}

Initial body proximate composition (g kg^{-1}) was 732.0 moisture, 160.1 protein, 71.9 lipid, 32.6 ash, 2.5 fiber and 3.4 carbohydrate. Initial gross energy was 18.50 kJ g^{-1}.† Carbohydrate = 1000 g kg^{-1} – (moisture + protein + lipid + ash). Different superscripts in rows indicate statistical significance at $P < 0.05$. Values are presented as mean±SEM (n=3).

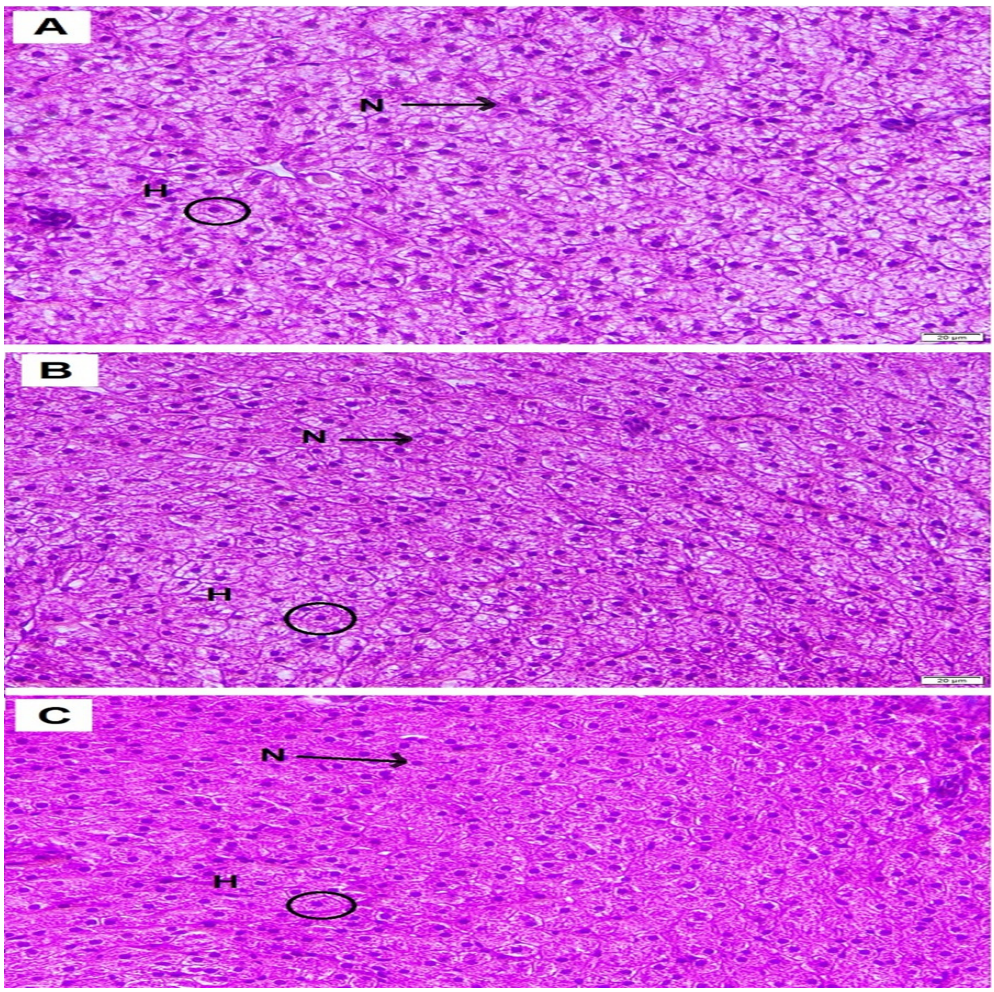

Figure 2: Liver histology of *T. tambroides* fingerlings fed with different carbohydrate complexity diets for 8 weeks; (A) starch, (B) sucrose, and (C) glucose. Magnification ×10; scale bar = 20µm. H, hepatocytes; N, nucleus.

DISCUSSION

The growth rate of *T. tambroides* observed across all treatments in this study was relatively slow, aligning with the species' inherent biological characteristics (Enes *et al*., 2010). Diets containing starch resulted in improved growth, body indices, and feed efficiency compared to those supplemented with glucose or sucrose. This agrees with the findings of Xu *et al*. (2020), who reported poor weight gain, and specific growth rate in brook trout, *Salvelinus fontinalis* fed dietary glucose or sucrose as compared to those fed diets with dextrin or pre-gelatinized corn starch. Nile tilapia also fed a glucose-based diet was reported to show lower weight gain compared to those fed on sucrose diet (Zhou *et al*., 2022). The poor utilization of glucose observed could be due to faster glucose absorption in the gut because of its simple molecular structure which can result in inefficient metabolism. In contrast, the absorption of starch with a complex molecular structure in the gut is slower and result in the suppression of the innate immunity, increased oxidative stress and distortion in glucose metabolism (Enes *et al*., 2011; Xu *et al*., 2020). Similar preferences for dietary starch over simple dietary carbohydrates were also observed in omnivorous freshwater fishes such as southern catfish, *Silurus meridionalis* (Fu 2005), hybrid tilapia, *Oreochromis niloticus* × *O. aureus* (Tung and Shiau 1993; Lin and Shiau 1995), and the gibel carp, *Carassius auratus gibelio* (Tan *et al*., 2009).

On the other hand, other omnivorous, freshwater cyprinids such as rohu, *Labeo rohita* and mrigal carp, *Cirrhinus mrigala* were found to better utilize dextrin, (a lesser complex carbohydrate than starch) for growth over glucose and sucrose (Erfanullah and Jafri 1995; Singh *et al*., 2006). The blunt snout bream, *Megalobrama amblycephala* is also reported to have a growth response to dextrin over higher complexity carbohydrates like cellulose, wheat starch, corn starch, and over simple carbohydrates like maltose, sucrose and glucose (Ren *et al*., 2015). These findings suggest that growth response to dietary carbohydrate forms may be species-dependent regardless of whether they are in the same family or not. In general, *T. tambroides*' poor use of glucose and sucrose for growth could be related to their low degree of energy metabolism. Fish may have a low rate of energy consumption and a high rate of energy supply when using carbohydrate as a fuel. The rate of energy supply may be overabundant after excessive glucose consumption, resulting in persistent hyperglycemia (Krishnan and Rohner, 2019). Many factors affecting dietary carbohydrate utilization in fish could be linked to this putative process, which requires further investigation. While the experimental diets were formulated to be isonitrogenous and isolipidic, proximate analysis revealed variations in the final composition. Specifically, the calculated carbohydrate content was significantly higher in the glucose (310.7 g kg^{-1}) and sucrose (319.9 g kg^{-1}) diets compared to the starch control (244.6 g kg^{-1}). This difference of approximately 66–75 g kg^{-1} in total carbohydrate content represents a limitation of this study, as the higher carbohydrate and energy load in the simple sugar diets could have acted as a confounding factor. Consequently, the poor growth performance and metabolic dysfunction observed in the glucose and sucrose groups might be influenced not only by carbohydrate complexity but also by the absolute amount of dietary carbohydrates.

Excess carbohydrates in vertebrates are converted to glycogen and lipids in adipose and liver tissues via cytosolic polymerisation (Kamalam *et al*., 2017). Our study showed that *T. tambroides* fed starch had a significantly higher HSI than those fed glucose. An increased hepatosomatic index (HSI) is a non-specific indicator of liver enlargement and may reflect hepatic glycogen accumulation, lipid deposition, or a combination of both rather than steatosis alone (Li *et al*., 2021). Therefore, the absence of steatosis in routine histological sections does not necessarily exclude carbohydrate-induced hepatomegaly or enlarged liver. In freshwater fish, excessive dietary starch has been associated with mixed hepatic lesions involving both glycogen and lipid accumulation. For example, dietary starch levels exceeding 100g kg^{-1} induced concurrent hepatic glycogen and lipid accumulation in largemouth bass (*Micropterus salmoides*) (Zhang *et al*., 2020), while high-starch feeding also increased the hepatopancreas index and promoted marked hepatic glycogen deposition accompanied by liver injury (Zhong *et al*., 2022). Likewise, excessive dietary starch can stimulate hepatic lipogenesis while suppressing fatty acid oxidation, further contributing to liver enlargement (Liu *et al*., 2023; Xie *et al*., 2024). Collectively, these studies indicate that elevated HSI should be interpreted as a general marker of altered hepatic energy storage rather than evidence of lipid accumulation alone.

Accordingly, the absence of steatosis in the present study does not contradict the observed increase in HSI. High-carbohydrate diets can induce glycogenic hepatopathy characterized by hepatocyte swelling and marked glycogen accumulation without significant hepatic lipid deposition (Zou *et al*., 2025), while routine hematoxylin and eosin staining may not detect mild lipid accumulation (Villasante *et al*., 2022). Furthermore, the low CRV does not preclude hepatic glycogen storage because excess glucose may be preferentially stored as liver glycogen (Li *et al*., 2021), whereas the high LRV suggests that enhanced lipogenesis may also have contributed to liver enlargement. Thus, the elevated HSI most likely reflects combined alterations in carbohydrate and lipid metabolism, with glycogen-

dominant hepatomegaly being the most plausible explanation unless confirmed otherwise by glycogen- or lipid-specific analyses (Li *et al*., 2021; Zou *et al*., 2025; Withyachumnarnkul *et al*., 2025). This agrees with the findings in blunt snout bream, *M. amblycephala* fed high dietary carbohydrates which recorded significantly higher values in HSI (Adjoumani *et al*., 2022), though it remains highly species-dependent as rainbow trout, *O. mykiss* (Pfeffer *et al*., 1991), and jundiá, *Rhamdia quelenand* (Corrêia *et al*., 2019) have shown no significant HSI differences across varying carbohydrate complexities.

The results from this experiment also showed that *T. tambroides* fed starch had higher PRV and ERV in accordance to Deng *et al*. (2005) where white sturgeon fed with starch diet had higher PRV and ERV than their glucose-fed counterparts. Similarly, jundiá fed diet with starch showed higher PRV compared to those fed diets containing fructose, sucrose and maltodextrin (Corrêia *et al*., 2019). PER value indicated that *T. tambroides* fed starch displayed a greater protein-sparing effect than fish fed glucose and sucrose, a similar effect was also described in the olive flounder, *P. olivaceus* (Lee *et al*., 2003). On the contrary, grass carp and Chinook salmon, *Oncorhynchus tshawytscha* can efficiently utilize glucose for protein-sparing (Tian *et al*., 2004; Araujo *et al*., 2023). Nonetheless, protein-sparing effect was not observed in gilthead sea bream, *Sparus aurata*, GIFT tilapia, and European sea bass, *D. labrax* when fed different carbohydrate complexities indicating that these species have similar efficiency for the utilization of both starch and glucose (Enes *et al*., 2006, 2008, 2010; Qiang *et al*., 2014). Furthermore, elucidating carbohydrate utilization in metabolic pathways, especially physiological responses to dietary energy from carbohydrates will be valuable in formulating a species-specific diet (Salati and Amir-Ahmady, 2001; Trushenski *et al*., 2006). Understanding the ideal carbohydrate form and complexity as an exogenous glucose source for dietary inclusion can spare the use of essential amino acids in gluconeogenesis pathway, thus encouraging the protein-sparing effect (Kamalam *et al*., 2017; Panserat *et al*., 2019).

CONCLUSION

The findings conclude that *T. tambroides* benefits from the inclusion of higher carbohydrate complexity in its diet, in comparison to simple carbohydrates like sucrose and glucose. Carbohydrate utilization is species-specific, and carbohydrate complexities is a regulating factor in fish physiological changes. This study also provides baseline formulation incorporating the use of starch, considering the complexity of different carbohydrates and their availability.

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NOVELTY STATEMENT

This study is the first to investigate the effects of dietary carbohydrate complexity on growth, feed utilization, and metabolic responses in *Tor tambroides*. Our results demonstrate a clear preference for complex starch over simple sugars (glucose and sucrose), leading to superior growth performance, body indices, feed efficiency, and protein-sparing effects.

The findings reveal species-specific metabolic traits, including poor simple-sugar utilization and elevated HSI primarily associated with glycogen accumulation rather than steatosis. These insights fill a key knowledge gap in the nutritional physiology of this slow-growing cyprinid and support the formulation of optimized, species-specific aquafeeds.

AUTHORS CONTRIBUTIONS

S.D.I conceived and designed the study, performed the feeding trial, laboratory analyses, data interpretation, statistical analysis and drafted the original manuscript. S.R contributed to data interpretation and critical revision of the manuscript. H.C, D.T. and O.V. T. assisted in manuscript revision, data curation and data interpretation. M.S.K. provided supervision, resources, and critical revision of the manuscript. All authors read and approved the final version of the manuscript.

Generative AI and AI assisted technology statement

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Conflict of interest

The authors has no conflicts of interest to declare regarding

the publication of this article.

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