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Adaptation of Nile tilapia (*Oreochromis niloticus*) to different levels of dietary carbohydrates: New insights from a long term nutritional study

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ABSTRACT

The objective of this study was to examine the long-term effects of different levels of dietary carbohydrates on glucose metabolism in the omnivorous Nile Tilapia (*Oreochromis niloticus*). Fish were fed from the first feeding stage until the adult stage, over a period of 40 weeks, using three different levels of carbohydrates (dextrin): 0% (CHO-L), 30% (CHO-M) and 50% (CHO-H). Growth performance, blood metabolite parameters, the proximate composition of the whole body, muscle and liver tissue, and the mRNA levels for genes involved in glycolysis, gluconeogenesis, lipogenesis and glucose transport in liver and muscle tissue were analyzed at week 26 and week 40. Fish fed the CHO-M diet exhibited the best growth performance, while the fish fed with the CHO-H diet showed the lowest growth performance. These data suggest that the incorporation of a certain level dietary carbohydrates can benefit Nile Tilapia. However, if the proportion of carbohydrates is very high, and concomitantly, the level of dietary proteins too low, this will not promote growth. Fish fed with carbohydrates exhibited a significant increase in lipid deposition in the whole body, muscle and liver tissues in. This seems to be due to increased lipogenic capacity, as reflected by higher hepatic fatty acid synthase mRNA levels and activity, as well as higher levels of plasma triglyceride. Nile Tilapia appear to be able to effectively adapt to the intake of carbohydrates, as reflected by: (i) the weak postprandial hyperglycemia (5.3–6.1 mM), (ii) the higher level of hepatic glycogen, (iii) the higher glycolytic pyruvate kinase enzyme in muscle (mRNA level and activity) and (iv) the inhibition of the gluconeogenic pathway for glucose-6-phosphatase and phosphoenolpyruvate carboxykinase enzymes (at molecular and enzymatic levels). Overall, these data show that the well-known differences in the capacity of carnivorous and omnivorous fish species to use dietary carbohydrates could be linked to differences in the regulation of the gluconeogenic and lipogenic pathways.

1. Introduction

Nile Tilapia (*Oreochomis niloticus*) is the most commonnly cultured tilapia species. A variety of culture systems can be used for tilapia farming, as tilapia are fast-growing fish, which are able to adapt to a wide range of environmental conditions, capable of reproducing in small ponds and are capable of consuming artificial feed from the first feeding stage. Global production of Nile Tilapia is predicted to continue to increase to sustain global demand. Recently, tilapia became the second most cultured fish after carp, which are farmed in over over 100 contries (FAO, 2018). To achieve least-cost production for global demand, nutritional research has facilitated the formulation of a cost-effective feed for tilapia farming, incorporating high levels of dietary carbohydrates. Nile Tilapia is an omnivorous grazer, which efficiently uses carbohydrates as a primary energy source (Kamalam et al., 2017). Nile Tilapia exhibit a high capability for using various carbohydrates, with carbohydrtaes accounting for 30%– 70% of thier diet depending on life stage (FAO, 2018). Metabolic responses to different dietary carbohydrate (dextrin) levels ranging from 0% to - 50% were recently demonstrated in adult Nile Tilapia (Boonanuntanasarn et al., 2018).

Carbohydrates are classified as non-essential nutrients for growth; however, they are commonly incorporated in aquafeeds, providing an energy source for fish. In general, fish vary in their ability to use carbohydrates as an energy source, both in digestion and metabolism,

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depending on their feeding habits (Kamalam et al., 2017). Carnivorous fish such as Rainbow Trout are less efficient in their use of carbohydrates (starch and dextrin), while omnivores (tilapia, Common Carp) and herbivores (Grass Carp) are better able to use dietary carbohydrates (Panserat et al., 2002; Wang et al., 2005; Figueiredo-Silva et al., 2013; Li et al., 2013; Azaza et al., 2015). In addition, carbohydrates could provide strong protein-sparing effects for growth in herbivorous and omnivorous fish, particularly in tilapia (Shiau and Peng, 1993). Integrated research is needed, not only to investigate the level of dietary carbohydrates that fish are able to use efficiently, but also to determine how dietary carbohydrates regulate intermediary metabolism, to develop precision nutrition for sustainable aquaculture.

Carnivorous fish are limited in their ability to use carbohydrates as an energy source. Metabolic responses of Rainbow Trout (carnivorous fish) have been intensively demonstrated (Polakof et al., 2012). Molecular regulation of metabolic pathways in the liver and muscles explain the low efficiency use of dietary carbohydrate results in a limited ability to inhibit hepatic gluconeogenesis, poor induction of hepatic lipogenesis and less effective cycling between glucose and glucose-6-phosphate in the liver. In addition, molecular regulation of glucose transport and glycolysis were absent in muscle tissue (Panserat et al., 2000, 2001, 2009; Polakof et al., 2012; Seiliez et al., 2011; Marandel et al., 2015; Kamalam et al., 2017). While explanations for the limited ability of carnivorous fish to use dietary carbohydrates have been intensively investigated, there is limited information available regarding how omnivorous fish have a high adaptability for carbohydrate use and there is no data when the fish were found from first feeding up to the adult stage. It has been suggested that an increase in lipogenesis and a decrease in gluconeogenesis enzyme activities could partly explain for the high efficiency use of dietary carbohydrates (Figueiredo-Silva et al., 2013). No clear molecular adaptation for hepatic glycolysis, gluconeogenesis and lipogenesis was observed when adult Nile Tilapia were fed with increased dietary carbohydrates (dextrin) at levels ranging from 0% to 50%, and molecular adaptation of glycolysis in muscle tissue was not clearly detectable (Boonanuntanasarn et al., 2018). Therefore, more intensive investigations are required to understand how tilapia can adapt their metabolism to dietary carbohydrates.

During this study, Nile Tilapia were fed for the first time with three semi-purified diets containing three different levels of digestible carbohydrates (dextrin) 0% (CHO-L), 30% (CHO-M) and 50% (CHO-H) over a 40 week period, from the first feeding stage to the adult stage. Molecular and enzymatic analyses of hepatic and muscular enzymes of glucose metabolism (and other metabolisms linked to carbohydrate ingestion) were obtained during the juvenile and adult stages after 26 or 40 weeks of rearing, respectively. In addition, data relating to growth performance, nutrient composition of tissues and blood metabolite parameters were also collected.

2. Materials and methods

2.1. Experimental design and diet formulation

The experimental design was completely randomized using three dietary carbohydrate levels, each of which was replicated six times. To test the effect of different dietary carbohydrate levels, the experimental diets were carbohydrate-low (CHO-L), carbohydrate-moderate (CHO-M) and carbohydrate-high (CHO-H) diets. Table 1 shows the ingredients of the three semi-purified diets (CHO-L, CHO-M, CHO-H) and their nutritive compsition (moisture, crude protein, crude fat, and ash content) as determined following standard AOAC methods (1990). The diets were isoenergetic and isolipid. The increase in dietary carbohydrates was concommitant with a decrease in dietary proteins. All test ingredients were obtained from commercial companies. The ingredients were pelleted and dried at 80°C for 4 h. All experimental diets were stored at −20°C until use.

Table 1
Ingredients and chemical composition (%) of the three experimental diets: carbohydrate-low (CHO-L), carbohydrate-moderate (CHO-M) and carbohydrate-high (CHO-H) diets.

Ingredients	CHO-L	CHO-M	CHO-H
Casein	82	57	32
Gelatin	7	7	7
Soybean oil	6	6	6
Dextrin	0	25	50
Dicalcium phosphate	1	1	1
Premix[a]	3	3	3
Vitamin C	1	1	1
Proximate composition (% dry weight)			
Dry Matter	88.3	88.7	88.6
Protein	63.4	45.7	27.4
Fat	6.2	6.2	6.2
Fiber	0.3	0.3	3.0
Ash	4.1	4.0	4.1
NFE[b]	14.4	32.6	50.7
total energy (kJ/g)	16.5	15.9	16.3

[a] Vitamin and trace mineral mix provided the following (IU kg^{-1} or g kg^{-1}diet): biotin, 0.25 g; folic acid, 0.003 g; inositol, 0.25 mg; niacin, 0.0215 g; pantothenic acid, 0.03 g; vitamin A, 5000 IU; vitamin B1, 0.0025 g; vitamin B2, 0.0012 g; vitamin B6, 0.0075 g; vitamin B12 0.00005 mg; vitamin C, 1 g; vitamin D3, 1000 IU; vitamin E, 100 IU; vitamin K, 0.008 g; copper, 0.02 g; iron, 0.2 g; selenium, 0.3 mg; zinc, 0.32 g.

[b] Nitrogen-free extract = Dry matter – (crude protein + crude lipid + crude fiber + ash).

2.2. Experimental fish and fish culture

The Nile Tilapia (*O. noliticus*, Chitrada 3) used in this study were all male fish. Newly hatched larvae were collected from the breeding pond at the Suranaree University of Technology Farm (Nakhon Ratchasima, Thailand). Eighteen hapa cages (1 × 1 × 1 m^3) (i.e. six replicates of three treatments) were maintained in cement ponds with a natural light–dark cycle (12:12 h light–dark cycle). One thousand and fifty newly hatched larvae (approximately 10 mg) were reared in each hapa. To investigate the long-term effects of different dietary carbohydrates, fish were fed the experimental diets from just after yolk-sac absorption (first feeding stage) through to the adult stage, over a 40 week period. During the first 4 weeks, swim-up fry were fed the experimental diet incorporated with 17α-methyltestosterone (60 mg/kg) five times daily (30% body weight during week 1, 20% body weight during week 2, and 10% body weight during weeks 3–4). Following this, fish were fed 3 of their body weight twice daily (09:00 and 16:00 h) until the end of the experimental period. To maintain an optimal stocking density, a density of 100 fish/hapa (within each replicate) was maintained between weeks 10 and 26. Subsequently, experimental fish were transferred to cement ponds (2 × 2 × 2 m^3), where the stocking density was maintained at 50 fish/pond during weeks 27–33, and at 25 fish/pond during weeks 34–40. Throughout the experimental period, fish were grown in dechlorinated tap water under continuous aeration. A flow-through water exchange system replaced one-third of the water every other week. Air and water temperatures were measured daily during the experimental period, and ranged from 19.0°C to 35.0°C and 21.5°C to 27.5°C, respectively. Dissolved oxygen content and pH were measured weekly using a dissolved oxygen meter and pH meter. The values were found to be within acceptable ranges of 6.78–6.80 and 7.80–7.84 mg L^{-1}, respectively.

2.3. Fish sampling and blood collection

At week 26 and week 40 fish were sampled 5 hafter feeding, as this time has been reported to correspond with peak postprandial glycemia (Boonanuntanasarn et al., 2018). Two fish from each diet replicate (n = 12 fish per experimental diet) were randomly selected and