

# Hepatic glucokinase and glucose-6-phosphatase responses to dietary glucose and starch in gilthead sea bream (*Sparus aurata*) juveniles reared at two temperatures

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## Abstract

The effects of carbohydrate sources/complexity and rearing temperature on hepatic glucokinase (GK) and glucose-6-phosphatase (G6Pase) activities and gene expression were studied in gilthead sea bream juveniles. Two isonitrogenous (50% crude protein) and isolipidic (19% crude lipids) diets were formulated to contain 20% waxy maize starch or 20% glucose. Triplicate groups of fish (63.5 g initial body weight) were fed each diet to near satiation during four weeks at 18 °C or 25 °C. Growth, feed intake, feed efficiency and protein efficiency ratio, were higher at the higher water temperature. At each water temperatures fish growth and feed efficiency were higher with the glucose diet. Plasma glucose levels were not influenced by water temperature but were higher in fish fed the glucose diet. Hepatosomatic index and liver glycogen were higher at the lower water temperature and within each water temperature in fish fed the glucose diet. No effect of water temperature on enzymes activities was observed, except for hexokinase and GK which were higher at 25 °C. Hepatic hexokinase and pyruvate kinase activities were not influenced by diet composition, whereas glucose-6-phosphate dehydrogenase activity was higher in fish fed the glucose diet. Higher GK activity was observed in fish fed the glucose diet. GK gene expression was higher at 25 °C in fish fed the waxy maize starch diet while in fish fed the glucose diet, no temperature effect on GK gene expression was observed. Hepatic G6Pase activities and gene expression were neither influenced by dietary carbohydrates nor water temperature. Overall, our data suggest that in gilthead sea bream juveniles hepatocytes dietary carbohydrate source and temperature affect more intensively GK, the enzyme responsible for the first step of glucose uptake, than G6Pase the enzyme involved in the last step of glucose hepatic release.

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## 1. Introduction

Protein, usually provided by fish meal, is the single most expensive ingredient in fish diets. Therefore, the high protein requirement for growth of carnivorous fish, as gilthead sea bream, makes dietary costs high and contributes to potential high nitrogenous wastes into the environment. The use of non-protein digestible energy sources such as carbohydrates is a way

of minimizing the above mentioned problems. However, in fish and particularly in carnivorous species, the utilization of digestible dietary carbohydrates for energy purposes appears limited (Wilson, 1994; Hemre et al., 2002; Stone, 2003) and a prolonged postprandial hyperglycemia has been observed after a carbohydrate-rich diet (Bergot, 1979b; Cowey and Walton, 1989; Wilson, 1994; Moon, 2001). Until now the basis for such apparent glucose intolerance are not fully understood. One possible explanation for the poor efficacy of digestible carbohydrates as energy source may be a disturbance of glucose homeostasis attributable to an unbalance between hepatic glucose phosphorylation by glucokinase (GK, EC 2.7.1.2) and glucose-6-phosphate hydrolysis, catalysed by glucose-6-phosphatase

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(G6Pase, EC 3.1.3.9) (Panserat et al., 2001). In mammals, GK and G6Pase expressions are respectively induced and repressed by dietary carbohydrates (Printz et al., 1993; van de Werve et al., 2000). In fish, the existence of a mammalian-like induction of GK expression by dietary carbohydrates has been demonstrated in the liver of Atlantic salmon *Salmo salar* (Tranulis et al., 1996), perch *Perca fluviatilis* (Borrebaek and Christophersen, 2000), rainbow trout *Oncorhynchus mykiss*, common carp *Cyprinus carpio*, gilthead sea bream (Panserat et al., 2000a) and European sea bass *Dicentrarchus labrax* (Enes et al., 2006a). Regarding G6Pase, although Shimeno et al. (1995) reported a decrease of enzyme activity with increasing dietary carbohydrate levels in common carp, a lack of G6Pase expression regulation by carbohydrates was observed in gilthead sea bream and in rainbow trout (Panserat et al., 2000b, 2001; Caseras et al., 2002).

Additional hypotheses to explain the low dietary glucose utilization in fish are: amino acids, especially arginine, that seems to be more potent stimulators of insulin secretion than glucose (Mommensen and Plisetskaya, 1991); relatively low numbers of muscle insulin receptors in fish as compared to mammals (Párrizas et al., 1994); low glucose phosphorylation capacity (Cowey and Walton, 1989) and low number of glucose transporters in fish muscle (Wright et al., 1998).

Carbohydrate utilization in fish may be influenced by many parameters such as carbohydrate sources and complexity (Wilson, 1994; Krogdahl et al., 2005). Although there is no discernable pattern in the ability of different species to utilize simple versus complex carbohydrates most fish species use dietary starch better than glucose (Furuichi and Yone, 1982; Lin and Shiau, 1995; Lee and Lee, 2004; Enes et al., 2006b). This may be due to the reported poor capacity of fish to utilize high levels of absorbed glucose (Panserat et al., 2001). In fact, a large portion of the absorbed glucose may be excreted before being effectively used at the cellular level (Deng et al., 2001).

Fish are ectothermic vertebrates that inhabit aquatic environments susceptible to seasonal and daily changes in water temperature. As a result, temperature modulates fish growth, feed utilization, nutrient digestibility and the activities of key enzymes of intermediary metabolism (Shimeno and Shikata, 1993; Brauge et al., 1995; Shikata et al., 1995; Kuz'mina et al., 1996; Médale et al., 1999; Peres and Oliva-Teles, 1999; Enes et al., 2006b). Data on the effect of water temperature on carbohydrate utilization is scarce. In rainbow trout, the efficiency of carbohydrates as energy suppliers improved with the increase of water temperature (Médale et al., 1991; Brauge et al., 1995). In common carp, Shikata et al. (1995) reported higher activities of key enzymes of glycolytic and gluconeogenic pathways at lower water temperatures which suggest a thermal compensation in low acclimation temperature. Finally, in European sea bass Enes et al. (2006b) observed enhanced liver glycolytic, gluconeogenic and lipogenic capabilities at higher water temperature.

According to our knowledge, no previous studies with gilthead sea bream are available comparing carbohydrate utilization at different water temperatures. Thus, the aim of the present study was to study the effect of two carbohydrate sources with different molecular complexities (waxy maize starch and glucose) on growth performance and on the activities

Table 1  
Composition and proximate analyses of the experimental diets

	Diets	
	WS	GLU
<i>Ingredients (dry weight basis)</i>		
Fish meal <sup>a</sup>	60.6	60.6
Soluble fish protein concentrate <sup>b</sup>	5.0	5.0
Cod liver oil	11.3	11.3
Waxy maize starch <sup>c</sup>	19.7	–
D-Glucose	–	19.7
Vitamin premix <sup>d</sup>	1.0	1.0
Mineral premix <sup>c</sup>	1.0	1.0
Choline chloride (60%)	0.5	0.5
Carboxymethylcellulose	1.0	1.0
<i>Proximate analyses (dry matter basis)</i>		
Dry matter (%)	88.4	84.7
Crude protein (%)	49.6	51.1
Crude fat (%)	18.5	19.3
Ash (%)	10.2	10.9
Gross energy (kJ g <sup>-1</sup> )	22.8	24.0

<sup>a</sup> TripleNine, Prime Quality, Denmark (CP: 73.3% DM; GL: 9.7% DM).

<sup>b</sup> Sopropêche G, France (CP: 73.0% DM; GL: 17.0%DM).

<sup>c</sup> Cerestar (Mechelen, Belgium).

<sup>d</sup> Vitamins (mg kg<sup>-1</sup> diet): retinol acetate, 18,000 (IU kg<sup>-1</sup> diet); cholecalciferol, 2000 (IU kg<sup>-1</sup> diet); alpha tocopherol acetate, 35; sodium menadione bisulphate, 10; thiamin–HCl, 15; riboflavin, 25; calcium pantothenate, 50; nicotinic acid, 200; pyridoxine HCl, 5; folic acid, 10; cyanocobalamin, 0.02; biotin, 1.5; ascorbic acid, 50; inositol, 400.

<sup>e</sup> Minerals (mg kg<sup>-1</sup> diet): cobalt sulphate, 1.91; copper sulphate, 19.6; iron sulphate 200; sodium fluoride, 2.21; potassium iodide, 0.78; magnesium oxide; 830; manganese oxide, 26; sodium selenite, 0.66; zinc oxide, 37.5; dibasic calcium phosphate, 5.93 (g kg<sup>-1</sup> diet); potassium chloride, 1.15 (g Kg<sup>-1</sup> diet); sodium chloride, 0.40 (g Kg<sup>-1</sup> diet).

and gene expression of key enzymes of glycolytic (GK) and gluconeogenic (G6Pase) pathways in gilthead sea bream juveniles reared at two water temperatures (18 °C and 25 °C).

## 2. Materials and methods

### 2.1. Diets

Two isonitrogenous (50% crude protein) and isolipidic (19% crude lipids) diets were formulated to contain 20% of either waxy maize starch (WS diet) or glucose (GLU diet). Waxy maize starch was obtained from Cerestar (Mechelen, Belgium) and D(+)-glucose from MERCK (Darmstadt, Germany). Waxy maize starch (99% amylopectin, 1% amylose) is a modified starch obtained through the use of techniques of genetic engineering that allows the manipulation of the amylose/amylopectin ratio. All dietary ingredients were finely ground, mechanically mixed with water at an inclusion level of 5% and dry pelleted in a laboratory pellet mill through a 3 mm dye. Ingredients and proximate composition of the experimental diets are presented in Table 1.

### 2.2. Fish rearing

Fish used in this study were gilthead sea bream (*S. aurata*) juveniles obtained from a commercial hatchery. The trial was

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