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Breeding selection of rainbow trout for high or low muscle adiposity differentially affects lipogenic capacity and lipid mobilization strategies to cope with food deprivation

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ABSTRACT

The present study evaluates the transcriptional regulation of lipid metabolism, adiponectin system and oxidative stress genes in two rainbow trout lines selected over seven generations for low (lean line, LL) or high (fat line, FL) muscle adiposity, and subjected to different fasting regimes. Under feeding conditions, FL fish had higher muscle lipid content, plasma triglycerides (TG) and non-esterified fatty acids (NEFAs) than the LL fish. Besides, FL fish had higher fatty acid synthase (*fasn*) mRNA levels in adipose tissue (AT) and white muscle (WM), and higher lipoprotein lipase (*lpl*) mRNA levels in WM, suggesting an increased lipogenic capacity and fatty acid uptake in the fatty genotype. In response to fasting, the two fish lines displayed a different trend in muscle lipid mobilization, plasma TG levels changes and lipid metabolism-related genes expression patterns. There were different *fasn* expression profiles between the fish lines in both, AT and WM, in agreement with the changes observed in plasma TG levels. The FL fish had higher adiponectin receptor 2 mRNA levels in WM and adiponectin mRNA levels in AT than LL fish after 1 and 4 weeks of fasting respectively, indicating a difference between genotypes in the adiponectin system. Furthermore, oxidative stress genes mRNA levels in both fish lines showed a different pattern between AT and WM upon fasting, probably indicating a higher protective effect in WM. Overall, the present study reveals a distinct metabolic regulation for each genotype, highlighting their different strategies in response to food deprivation.

1. Introduction

Energy homeostasis is a critical mechanism by which animals regulate food intake and energy expenditure. When this equilibrium is disrupted such as during fasting or overfeeding, physiological and behavioral compensatory changes take place to restore and maintain energy balance (Galgani and Ravussin, 2008; Wang et al., 2006). As a major source of energy storage, adipose tissue (AT) is considered to play an important role in the regulation of whole-body energy homeostasis (Viscarra and Ortiz, 2013). In addition, AT is an important endocrine tissue secreting a great variety of hormones such as leptin and adiponectin (Kershaw and Flier, 2004; Khan and Joseph, 2014). In mammals, the contribution of these adipokines in regulating energy balance during food restriction is well documented (Gui et al., 2003; Pénicaud, 2010). Adiponectin is involved in the modulation of glucose and lipid metabolism (Chandran et al., 2003), and decreased circulating levels of this adipokine are associated with obesity while increased levels are found in fasting patients (Pannacciulli et al., 2003). Furthermore, its anti-inflammatory role has been shown to display protective actions on the development of several metabolic disorders (Bianco et al., 2013).

In their natural environment, fish can experience prolonged periods of fasting, either as a result of spawning migration or seasonally limited food availability (Byström et al., 2006; McCue, 2010). To survive these periods, fish can metabolize large proportions of their energy reserves without permanent physiological harm (Navarro and Gutiérrez, 1995; Wieser et al., 1992), highlighting their particular suitability as subjects for studies on the effects of long-term fasting. Moreover, for aquaculture production purposes, dietary manipulation in feeding programs

Abbreviations: AT, adipose tissue; FL, fat line; LL, lean line; WM, white muscle; LSI, liver somatic index; VSI, visceral somatic index; ROS, reactive oxygen species

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has been explored, such as subjecting the animals to different periods of fasting, not only in order to induce compensatory growth during subsequent feeding periods, but also to improve product/flesh quality before sacrifice (Rasmussen et al., 2000; Won and Borski, 2013). The molecular mechanisms regulating growth and catabolism have been studied in fish (Ibarz et al., 2007; Johansson et al., 2016; López-Luna et al., 2016; Navarro and Gutiérrez, 1995), but there are still many caveats concerning their response to fasting, especially in terms of regulatory functions of relatively recently discovered adipokine hormones such as adiponectin.

In salmonids, the main energy sources mobilized during fasting are lipids stored in visceral AT, liver and muscle, whereas tissue protein is only mobilized, chiefly from muscle, during long-term starvation periods (Bar and Volkoff, 2012; Bower et al., 2009). Salmonids are regarded as "fatty" fish as they store significant amounts of lipids in muscle. Muscle fat content of farmed rainbow trout (*Oncorhynchus mykiss*) fillet is typically 12–18% (Davidson et al., 2014), depending on intrinsic factors, such as genotype and sexual maturation, as well as extrinsic factors such as environmental or rearing conditions (Weil et al., 2013).

The mobilization of body reserves upon food deprivation in fish is tightly linked to a reduction in metabolic rate as an energy-saving mechanism. However, such metabolic changes can be associated with higher oxidative stress (Feng et al., 2011), as mitochondria involved in the metabolic responses to fasting also produce damaging reactive oxygen species (ROS). As studies regarding the influence of fasting on antioxidant defenses in liver and flesh lipid oxidation at the molecular level are still scarce (Pascual et al., 2003; Zhang et al., 2007), elucidation of the effects of fasting on rainbow trout lipid metabolism, the adiponectin system regulation and oxidative stress status is of particular interest.

Although controversial, the "thrifty genes" hypothesis postulates that some individuals favor increased fat deposition capacity, in order to explain differential metabolic responses to diverse environmental stressors, such as food deprivation (Chakravarthy and Booth, 2003; Neel, 1962). Irrespective of the merit of this hypothesis, there is clearly large individual variability in metabolic strategies depending on several factors such as age, sex, body size or genetic background. These specific contributions to metabolic phenotypes and diseases have been investigated in mammals (Holmes et al., 2008; Li et al., 2016; Masson et al., 2003), but rarely in fish (Metcalfe et al., 2016), even though there is an increased interest within the aquaculture industry to select for specific physiological traits to obtain optimal fish phenotypes.

An important quality trait in farmed salmonids is muscle adiposity, as this can affect organoleptic characteristics as well as yield of the fillets (Bugeon et al., 2010). Breeding selection of rainbow trout for high or low muscle adiposity has shown this parameter to be a highly heritable trait (Quillet et al., 2005). Through subsequent generations, two rainbow trout lines selected for low (lean line, LL) and high (fat line, FL) muscle adiposity have also diverged in several aspects of glucose and lipid metabolism (Kamalam et al., 2012; Kolditz et al., 2008; Skiba-Cassy et al., 2009). Thus, the FL fish have higher capability than the LL fish to utilize and store glucose and maintain its homeostasis (Jin et al., 2014a; Kolditz et al., 2008). Further, enhanced lipogenic potential is suggested to be a key mechanism responsible for high muscle adiposity in FL fish (Jin et al., 2014b). The experiment on which the current study is based was carried out in 2014 on the seventh generation of the breeding selected FL and LL rainbow trout, and both systemic and central effects of leptin endocrinology in relation to energy stores and lipid mobilization have been analyzed (Gong et al., 2016; Johansson et al., 2016). However, the role of adipose tissue in the regulation of lipid homeostasis in these lines has not been studied in detail.

The aim of the current study was to elucidate relationships between lipid metabolism, oxidative stress and the adiponectin system by comparing important lipid parameters and expression of key genes in LL and FL rainbow trout during feeding and fasting. As previous studies have reported line-dependent differences in the regulation of metabolic processes such as glucose utilization or some lipid metabolism markers under normal feeding conditions, the hypothesis is that these lines may also follow different strategies to cope with fasting, especially in white muscle (WM) and AT.

2. Materials and methods

2.1. Experimental fish and culture conditions

Adult rainbow trout, approximately 250 g in weight, were maintained at the Institut National de la Recherche Agronomique (INRA) experimental facilities in the Pisciculture Expérimentale des Monts d'Arrée (PEIMA) (Drennec, Sizun, France). Animals were kept in 1.8 m^3 circular outdoor tanks with water flow of 3 $m^3 h^{-1}$ and oxygen levels > 6.0 mg L^{-1}, under ambient light and temperature conditions (from 10.6 to 13.5 °C), and fed five times per day with a commercial diet (B-MEGA-20, pellet size 5, containing 40% protein, 28% fat, and 20.5 MJ kg^{-1} of digestible energy; Le Gouessant, France; aqua.-legouessant.com). Daily ration was calculated every week based on fish size and water temperature (from 1.16 to 1.25% body weight (BW) day^{-1}). All animal handling procedures complied with the Guidelines of the European Union Council Directive of 24 November 1986 (86/609/EEC), under the official license of L. Laurent (29–036). The PEIMA facility is approved for animal experimentation through license C29-277-02.

2.2. Experimental design and sampling

The present study was performed using two lines of rainbow trout obtained after seven generations of divergent selection for high or low muscle fat content, designated as fat line (FL) and lean line (LL), respectively (Quillet et al., 2005). The experimental design has been described in detail in Johansson et al. (2016). Briefly, the experiment was initiated by stocking 50 fish into each of 16 circular, outdoor tanks under the conditions described in Section 2.1. Eight tanks were stocked with FL fish of 238 ± 3 g BW and eight tanks with LL fish of 262 ± 3 g BW. After three-week acclimation period, a four-week experimental protocol was initiated, with the fish divided among four feeding/fasting regimes. Thus, each feeding/fasting regime included randomly assigned duplicate tanks of LL fish and of FL fish. The "control" regime included no fasting (0W), with the fish fed normally throughout. A second regime consisted of normal feeding for three weeks followed by one week of fasting (1W). A third regime consisted of two weeks of normal feeding followed by two weeks of fasting (2W), and the fourth regime consisted of fasting throughout (4W). The four regimes were initiated one day apart, to allow for final sampling being carried out in the same order, over four consecutive days, four weeks later. At sampling, ten fish per tank (two tanks per group), thus 20 LL fish and 20 FL fish per feeding/fasting regime, were randomly netted and anesthetized with a lethal dose (160 mg L^{-1}) of isoeugenol (ScanAqua, Norway) and sampled. BW was measured and the normally fed LL fish were 488 ± 33 g and the FL fish were 366 ± 17 g. Growth details of the other groups can be found in Johansson et al. (2016). Blood was taken from the caudal vessels and immediately placed on ice and centrifuged at 800 × *g* for 5 min at 6 °C and the plasma obtained was frozen at −20 °C. The whole liver and viscera (including gastrointestinal tract and visceral AT, but removing all gastric and intestinal content) were taken and weighed in order to obtain the liver and visceral somatic indexes (LSI and VSI, respectively, calculated as organ weight as percentage of BW). Pieces of epaxial WM were sampled from the right side of the fish immediately cranial to the dorsal fin and perivisceral AT samples were taken and snap-frozen in liquid nitrogen. All samples were subsequently transported and stored at −80 °C pending analysis.

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