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Deposition and mobilization of lipids varies across the rainbow trout fillet during feed deprivation and transition from plant to fish oil-based diets

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ABSTRACT

Identifying aquaculture feeding strategies that reduce the consumption of fish oil without sacrificing the cardioprotective lipid profile of the salmonid fillet will improve aquafeed economics and sustainability. Transitioning fish from a plant oil-based diet to a finishing diet rich in fish oil and long chain n-3 fatty acids (LCn3) for several weeks prior to harvest is effective at boosting the fatty acid profile of the whole salmonid fillet. This study determined whether the response to short-term feed deprivation and a finishing diet varies across different regions of the triploid rainbow trout fillet. Fish were placed on one of three feeding treatments: 1) FO: a fish oil (FO) diet for the entirety of the 20-week study, 2) VO/FO: a vegetable oil (VO) diet between weeks 1–12 then the FO diet for the final eight weeks, or 3) VO/fd/FO: the VO diet between weeks 1–12 followed by a two week period of feed deprivation before transitioning to the FO diet for the final six weeks. Fillets were divided horizontally into three sections (ventral, central, and dorsal) and the fatty acid profile of each was determined. There were unique responses to feed deprivation across fillet regions; the central region exhibited a loss of fatty acids, the dorsal region gained fatty acids, but there was no net gain or loss of fatty acids in the ventral region. The ventral and dorsal regions responded similarly to a high-FO finishing diet, increasing concentrations of fatty acids and LCn3, although not to levels observed in the FO treatment group. In contrast, the fatty acid profile in the central region remained largely unaffected by the finishing diet, with the exception of LCn3 in the VO/FO group that increased to levels comparable to the FO-treatment group. Expression of genes related to muscle atrophy (*fbxo32*) and LCn3 metabolism (*fads5*) also varied across different fillet regions and in response to dietary treatments. This study provides evidence for spatially distinct regulation of muscle growth and lipid metabolism that support region-specific physiological and metabolic responses to feeding strategies.

1. Introduction

Increased dietary fish intake is associated with reduced incidence of cardiovascular disease (Albert et al. 1998; Burr et al. 1989; Daviglus et al. 1997; Kris-Etherton et al. 2003a; Kris-Etherton et al. 2003b). There is strong support for a role of long chain n-3 polyunsaturated fatty acids (LCn3), defined as n-3 polyunsaturated fatty acids (PUFA) ≥20 carbons in length, in this response (Calder 2006; Calder 2010; Vykoukal and Davies 2011), thereby suggesting that consumption of fish with high fillet concentrations of LCn3, such as farmed rainbow trout (Blanchet et al. 2005), have benefits for cardiovascular health. High fillet LCn3 in most fish is a direct result of their consumption of diets containing high levels of fish oils derived from captured marine sources. However, economic and environmental concerns regarding the high demand of the aquafeed industry on these marine sources are driving the partial replacement of fish oil in aquafeeds with plant-derived oils (Tacon and Metian 2008; Turchini et al. 2009). While the growth performance of the fish is generally not affected, the lipid profile of the fillet largely mirrors that of the diet, and plants are notoriously poor sources of LCn3. Therefore, increasing the inclusion of plant oils in aquafeeds can compromise the nutritional benefits of fish like rainbow trout and Atlantic salmon that have high-LCn3 fillets with cardioprotective benefits (Rosenlund et al. 2010). For this reason, research efforts are focused on the development of feeding strategies that reduce reliance upon fish oil, contribute to improving sustainability, and improve the fillet LCn3 lipid profile.

A feeding strategy successful at increasing the fillet LCn3 concentrations in salmonids that consumed diets with high plant oil/low LCn3 is to transition fish to a high fish oil/high LCn3 finishing diet in the weeks prior to harvest (Codabaccus et al. 2013; Francis et al. 2014;

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Jobling 2004; Stone et al. 2011; Thanuthong et al. 2011a). However, the success of a finishing diet at restoring LCn3 is dependent on several factors, including the lipid profile of the plant oil diet, length of the finishing period, fillet fat content, and environmental variables such as temperature. For salmonid species that exhibit higher levels of fillet lipids, the dilution model of lipid gain is suitable for predicting changes in the fillet lipid profile upon consumption of a finishing diet (Jobling 2004; Robin et al. 2003). The model is most accurate for predicting changes in fatty acids of high abundance in neutral lipids like triacylglycerols (TAG), rather than polar lipids (PL) like membrane-bound phospholipids. The premise is that reductions in concentrations of plant-derived fatty acids like the 18:1 isomers are largely driven by dilution since TAG are subject to low turnover during continual feeding (Jobling 2004). Fitting with this model, short periods of feed deprivation prior to transitioning to a finishing diet have been tested as an approach to reduce TAG stores and further improve LCn3 deposition. Although this approach is costly for weight gain, it does enhance the capacity for LCn3 deposition in rainbow trout fillets (Thanuthong et al. 2012) but not in Murray cod (Palmeri et al. 2009).

Studies investigating the effectiveness of the finishing diet strategy have examined the response of the fillet as a single unit. However, the deposition and mobilization of lipids varies across different regions of the fillet. The ventral region of the fillet that covers the visceral cavity has a lipid concentration approximately double that of the dorsal and central regions, and three times higher than the caudal region of the fillet (Katikou et al. 2001; Kinsella et al. 1977; Testi et al. 2006; Toussaint et al. 2005). Adipocytes rich in TAG accumulate in myosepta, the thickest of which are in the ventral region (Zhou et al. 1995), so the TAG to PL ratio also differs across the fillet. Mobilization of lipids during an energy challenge induced by spawning is greatest in the central and ventral regions while the dorsal region is more resistant to lipid loss (Cleveland et al. 2017). However, fatty acid species, in terms of percent representation, exhibit only minor variation between regions (Cleveland et al. 2017; Testi et al. 2006). Thus far it has not been determined whether changes in the lipid profile in response to feeding strategies that aim to increase fillet LCn3 content vary across different fillet regions. This objective of this study was to determine if a finishing diet strategy, both with and without a feed deprivation period, affects lipid distribution across different regions of the triploid rainbow trout fillet. In addition, the expression of genes important for bioconversion of LCn3 was analyzed to investigate differential regulation of lipid synthesis between regions.

2. Methods

2.1. Animal husbandry

Triploid, female rainbow trout eyed eggs were obtained from Troutlodge (Sumner, WA) and hatched and raised at the USDA/ARS National Center for Cool and Cold Water Aquaculture (NCCCWA, Kearneysville, WV). Procedures and protocols involving live fish received approval from the NCCCWA Animal Care and Use Committee (IACUC) and were performed according to IACUC guidelines (protocol #108). Water alternated between flow-through and partial reuse (< 30%) and temperatures ranged between 12.0 and 13.5 °C. All tanks were indoors with artificial lighting that mimicked ambient photoperiod. Prior to the study fish consumed a commercially available feed (Finfish G, Zeigler Bros, Inc., Gardners, PA) and were reared according to standard husbandry procedures.

2.2. Experimental design

Triploid, female rainbow trout (~10 months, 250.2 ± 4.0 g) were randomly distributed among nine circular tanks (0.9 m^3 capacity), with 39 fish per experimental tank. Two custom diets were produced by a commercial feed producer (Zeigler Bros., Inc) for use in this study (Table 1). The FO diet utilized fish oil (FO) as the sole lipid source while the vegetable oil (VO) diet was produced with three different lipid sources (12% fish oil, 41% canola oil, and 41% flaxseed oil). Both diets were formulated to contain 42% crude protein and 18% crude fat.

Table 1
Diet formulation (g per 100 g diet). Fish oil (FO), vegetable oil (VO).

Ingredient	FO diet	VO diet
MENH 62% spec select	18.50	18.50
Poultry byproduct meal	18.00	18.00
Wheat flour	15.82	15.82
HP 300 soya protein	9.00	9.00
Whole wheat	8.00	8.00
Blood meal 92%	6.55	6.55
Canola Oil	–	5.50
Flaxseed oil	–	5.50
Soybean meal	5.00	5.00
Corn gluten 60%	4.65	4.65
Fish oil	13.32	2.32
Limestone	0.50	0.50
ARS 702 vit premix[a]	0.20	0.20
Choline Cl-70%	0.18	0.18
Amonex aqua dry	0.10	0.10
USFWS #3 min premix[b]	0.10	0.10
Tiger C-35	0.06	0.06
DL methionine	0.02	0.02
Calculated totals		
Crude protein	42.00	42.00
Crude lipid	17.98	17.98
Crude fiber	1.33	1.33
Moisture	9.09	8.98
Ash	7.93	7.92

[a] Contributed (per kg diet): vitamin A, 9650 IU; vitamin D, 6600 IU; vitamin E, 132 IU; vitamin K3, 1.1 g: thiamine mononitrate, 9.1 mg; riboflavin, 9.6 mg; pyridoxine hydrochloride, 13.7 mg; pantothenate dl-calcium, 46.5 mg; cyanocobalamin, 0.03 mg; nicotinic acid, 21.8 mg; biotin, 0.34 mg; folic acid, 2.5 mg; inositol, 600 mg.

[b] Contributed (mg per kg diet): calcium, 0.037; copper, 1.54; iodine, 10; iron, 0.6; magnesium, 0.22; manganese, 22.9; phosphorus, 0.0002; selenium, 0.0004; sodium, 0.0005; sulfur, 0.75; and zinc, 75.

Tanks were assigned to one of three treatment groups: 1) FO, 2) VO/fd/FO, and 3) VO/FO (Fig. 1A, n = 3 tanks per treatment). The FO treatment group was fed only the FO diet for the entire 20 week study. The VO/fd/FO treatment group was fed the VO diet from week 1 to 12, was feed deprived during weeks 13 and 14, then was fed the FO diet through week 20. The VO/FO treatment transitioned fish immediately to the FO finishing diet after the initial 12 weeks of VO diet consumption. Diets were provided using automatic feeders (Arvotec) programmed to dispense feed at a fixed percent of tank biomass (1.25–1.5%). The percentage was identical across all tanks and approached satiation, with the exception of the two week feed deprivation period. Cumulative feed conversion ratio (FCR) was calculated for each tank by dividing total feed intake by total biomass gain.

Fish were anesthetized with tricaine methanesulfonate (MS222, 100 mg/L) and individually weighed at the beginning of the study (week 1) and at the end of weeks 6, 12, 14, and 20. Feed was withheld the day of sampling. During sampling at weeks 12, 14, and 20, three random fish from each tank were euthanized with MS222 (300 mg/L). Livers were excised and skinless fillets were harvested. The fillets were partitioned into three regions by making two longitudinal cuts approximately 1 cm dorsal and ventral of the lateral line (Figs. 1B,C). The three regions are defined as the 1) ventral, 2) central, and 3) dorsal fillet region. Subsamples of white muscle were removed from each region of the left-side fillet and immediately frozen in liquid nitrogen for gene expression analysis. The regions from the right-side fillet were retained in their entirety for fatty acid analysis. All samples were stored at −80 degrees C until analysis.

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