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Effect of dietary conjugated linoleic acid (CLA) on lipid composition, metabolism and gene expression in Atlantic salmon (*Salmo salar*) tissues

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Abstract

Dietary conjugated linoleic acid (CLA) affects fat deposition and lipid metabolism in mammals, including livestock. To determine CLA effects in Atlantic salmon (*Salmo salar*), a major farmed fish species, fish were fed for 12 weeks on diets containing fish oil or fish oil with 2% and 4% CLA supplementation. Fatty acid composition of the tissues showed deposition of CLA with accumulation being 2 to 3 fold higher in muscle than in liver. CLA had no effect on feed conversion efficiency or growth of the fish but there was a decreased lipid content and increased protein content after 4% CLA feeding. Thus, the protein:lipid ratio in whole fish was increased in fish fed 4% CLA and triacylglycerol in liver was decreased. Liver β-oxidation was increased whilst both red muscle β-oxidation capacity and CPT1 activity was decreased by dietary CLA. Liver highly unsaturated fatty acid (HUFA) biosynthetic capacity was increased and the relative proportion of liver HUFA was marginally increased in salmon fed CLA. CLA had no effect on fatty acid Δ6 desaturase mRNA expression, but fatty acid elongase mRNA was increased in liver and intestine. In addition, the relative compositions of unsaturated and monounsaturated fatty acids changed after CLA feeding. CLA had no effect on PPARα or PPARγ expression in liver or intestine, although PPARβ2A expression was reduced in liver at 4% CLA feeding. CLA did not affect hepatic malic enzyme activity. Thus, overall, the effect of dietary CLA was to increase β-oxidation in liver, to reduce levels of total body lipid and liver triacylglycerol, and to affect liver fatty acid composition, with increased elongase expression and HUFA biosynthetic capacity.
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1. Introduction

Conjugated linoleic acid (CLA) is a term used to describe positional and geometric isomers of linoleic acid (18:2n-6; LA), the two main naturally occurring isomers being *cis*-9, *trans*-11 and *trans*-10, *cis*-12. These compounds occur particularly in beef and dairy products but are widespread at lower levels in many foodstuffs (Chin et al., 1992; Pariza et al., 2001). Dietary inclusion of CLA can cause significant alterations in energy and lipid metabolism in mammals leading to reductions in overall body fat mass. This has been suggested to be a positive effect in a variety of farmed species and animal disease models and by extension, humans (Belury, 2002; Thiel-Cooper et al., 2001; Wang and Jones, 2004). However, there are notable species differences in the tissue-specific pattern of effects caused by CLA. For example feeding CLA can be accompanied by accumulation of lipid in mouse liver and the development of lipodystrophy and insulin resistance (Tsuboyama-Kasaoka et al., 2000; Clement et al., 2002), whereas these deleterious effects are not observed in hamster, *Mesocricetus auratus* (Bouthegourd et al., 2002; Macarulla et al., 2005). CLA has also been shown to alter highly unsaturated fatty acid (HUFA) biosynthesis in cellular models (Chuang et al., 2001a,b; Eder et al., 2002), and to increase expression of genes involved in the HUFA biosynthetic pathway (Takahashi et al., 2003). The mechanisms of

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action of CLA in mammals are unclear, and few studies on CLA in non-mammalian species have been undertaken. However, the effects induced by CLA feeding on mammalian fat deposition and HUFA biosynthesis may be of considerable interest to the finfish aquaculture industry. This is because current practise in aquaculture, and particularly Atlantic salmon aquaculture, can lead to excess deposition of fat in the muscle of farmed fish (Sargent et al., 2002). In addition, the global limit on the supply of fish oil (Naylor et al., 2000) is driving the replacement of fish oils with plant-derived oils in aquaculture diets (Bell et al., 2005). This has raised concern regarding the potential for reducing levels of human health-promoting n-3 HUFA in farmed fish (Sargent and Tacon, 1999). The aim of the present study is to investigate the effects of dietary CLA on lipid metabolism, HUFA biosynthesis and lipid composition in the liver and muscle of Atlantic salmon (*Salmo salar*). The results are discussed in relation to observations in mammals and with regard to the potential use of CLA in aquaculture diets.

2. Materials and methods

2.1. Fish and diets

Three diets (4 mm pellets) containing CLA at inclusion levels of 0%, 2% and 4% were prepared at the Nutreco Technology Centre, Stavanger, Norway. The diets were formulated to satisfy the nutritional requirements of salmonid fish (U.S. National Research Council, 1993), and had the same basal composition containing 47% protein and 33% lipid, consisting of fish meal (55%), corn gluten (10%), wheat (8.3%), oil (26.3%), mineral and vitamin mixes (0.2%) and carophyl pink® (0.06%). The oils used were fish oil (Anchovy oil, Skretting, Stavanger, Norway), either alone or in combination with CLA (Tonalin® FFA80, containing 81% CLA free fatty acid as a 50:50 mixture of *cis* 9, *trans* 11 and *trans* 10, *cis* 12 isomers; Natural ASA, Sandvika, Norway) which replaced fish oil to the level of 2% and 4% of the total diet. The fatty acid compositions of the experimental diets are given in Table 1. Seven hundred and fifty Atlantic salmon post-smolts, average mass 132 g, were distributed randomly into three 2×2 m tanks (250/tank) at the Nutreco Aquaculture Research Centre, Lerang Research Station, Stavanger, Norway. Twenty fish per tank were PIT-tagged by implanting a micro-transponder into the peritoneal cavity. The fish were adapted to the new environment for 3 weeks before feeding the experimental diets. During the adaptation period, the fish received commercial diet (Atlantic 4 mm; Skretting). Feed intake was monitored during this period, and the trial did not start until appetite was at least 0.8% body weight. After the adaptation period, the fish were fed the experimental diets to satiation according to usual procedures at Lerang Research Station, for a period of 4 months. Feed intake was monitored throughout the trial and waste feed was collected from the effluent water from each tank by a wire mesh collector and dried. Feed given, waste feed and the resulting net feed intake were registered daily. Any mortalities were collected daily. The tanks were supplied with sea water at constant temperature (7.9 °C±0.1 °C). The oxygen level varied between 8 and 12 ppm, with an average of 9.9 ppm. A photoperiod of 18 h light and 6 h darkness was applied.

2.2. Sampling protocols

At the start and end of the trial, all the fish in each tank were anaesthetised with metacain (50 mg/L), individually weighed and measured. At the end of the trial, 20 fish per dietary treatment were sampled for compositional, enzymatic and molecular analyses, with 3 whole fish frozen immediately on dry ice and subsequently stored at −20 °C for whole body compositional (proximate) analyses. The other sampled fish were eviscerated and twelve used for biometric determinations (hepato-, viscero- and gonado-somatic index) and for lipid analyses. Muscle samples (Norwegian quality cut) and livers were taken from each fish, pooled in four pools of 3 fish each, and frozen immediately in liquid nitrogen (livers) or dry ice (muscle). Samples of liver, white muscle (WM), red muscle (RM) and intestine were dissected from the remaining 5 fish for molecular and biochemical analyses. Specifically, samples of 0.5 g of liver and intestine (pyloric caeca) were rapidly dissected into 5 ml of TriReagent (Sigma, Poole, UK) and immediately homogenised using an Ultra-Turrax tissue disrupter (Fisher Scientific, Loughborough, UK), and then frozen in liquid nitrogen for RNA analyses. In addition, samples of 1–2 g of liver, WM and RM for biochemical analyses were immediately frozen in liquid nitrogen. All samples

Table 1
Fatty acid compositions (percentage of weight) of experimental diets

	Fish oil	2% CLA	4% CLA
14:0	7.4	6.9	6.5
16:0	18.7	17.7	16.9
18:0	3.9	4.0	4.0
Total saturated[1]	30.9	29.3	28.0
16:1n-7	7.5	7.1	6.4
18:1n-9	8.8	9.5	10.0
18:1n-7	2.7	2.7	2.6
20:1[2]	3.3	2.7	2.7
22:1[3]	3.5	2.9	2.9
24:1n-9	0.5	0.6	0.5
Total monoenes	26.3	25.5	25.1
18:2 n-6	3.5	3.8	3.7
CLA (9c,11t)	0.0	1.9	4.6
CLA (10t,12c)	0.0	1.9	4.5
20:4 n-6	0.9	0.9	0.8
Total n-6PUFA[4]	4.7	8.8	13.9
18:3 n-3	1.2	1.2	1.1
18:4 n-3	3.4	3.1	2.9
20:4 n-3	0.8	0.8	0.7
20:5 n-3	14.7	13.8	12.5
22:5 n-3	1.7	1.6	1.4
22:6 n-3	16.3	15.9	14.4
Total n-3PUFA	38.1	36.4	33.0
Total PUFA	42.8	45.2	46.9

Data are means of analyses of two samples, each of which contained pellets pooled from three bags. Variation between the duplicate pools was less than 5%. [1], contains 15:0 and 17:0, present in some samples at up to 0.5%; [2], predominantly n-9 isomer; [3], predominantly n-11 isomer; [4], totals include 20:2n-6 present at up to 0.3%. CLA, conjugated linoleic acid; PUFA, polyunsaturated fatty acid.

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