

Effect of diets enriched in $\Delta 6$ desaturated fatty acids ($18:3n-6$ and $18:4n-3$), on growth, fatty acid composition and highly unsaturated fatty acid synthesis in two populations of Arctic charr (*Salvelinus alpinus* L.)

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Abstract

This study aimed to test the hypothesis that diets containing relatively high amounts of the $\Delta 6$ desaturated fatty acids stearidonic acid (STA, $18:4n-3$) and γ -linolenic acid (GLA, $18:3n-6$), may be beneficial in salmonid culture. The rationale being that STA and GLA would be better substrates for highly unsaturated fatty acid (HUFA) synthesis as their conversion does not require the activity of the reputed rate-limiting enzyme, fatty acid $\Delta 6$ desaturase. Duplicate groups of two Arctic charr (*Salvelinus alpinus* L.) populations with different feeding habits, that had been reported previously to show differences in HUFA biosynthetic capacity, were fed for 16 weeks on two fish meal based diets containing 47% protein and 21% lipid differing only in the added lipid component, which was either fish oil (FO) or echium oil (EO). Dietary EO had no detrimental effect on growth performance and feed efficiency, mortalities, or liver and flesh lipid contents in either population. The proportions of $18:2n-6$, $18:3n-3$, $18:3n-6$, $18:4n-3$, $20:3n-6$ and $20:4n-3$ in total lipid in both liver and flesh were increased by dietary EO in both populations. However, the percentages of $20:5n-3$ and $22:6n-3$ were reduced by EO in both liver and flesh in both strains, whereas $20:4n-6$ was only significantly reduced in flesh. In fish fed FO, HUFA synthesis from both $[1-^{14}\text{C}]18:3n-3$ and $[1-^{14}\text{C}]20:5n-3$ was significantly higher in the planktonivorous Coulin charr compared to the demersal, piscivorous Rannoch charr morph. However, HUFA synthesis was increased by EO in Rannoch charr, but not in Coulin charr. In conclusion, dietary EO had differential effects in the two populations of charr, with HUFA synthesis only stimulated by EO in the piscivorous Rannoch morph, which showed lower activities in fish fed FO. However, the hypothesis was not proved as, irrespective of the activity of the HUFA synthesis pathway in either population, feeding EO resulted in decreased tissue levels of $n-3$ HUFA and $20:4n-6$. This has been observed previously in salmonids fed vegetable oils, and thus the increased levels of $\Delta 6$ desaturated fatty acids in EO did not effectively compensate for the lack of dietary HUFA.

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1. Introduction

Omega-3 (or $n-3$) polyunsaturated fatty acids (PUFA) are important dietary nutrients for mammals including humans (Simopoulos, 2000), and fish are the major dietary source of $n-3$

highly unsaturated fatty acids (HUFA) (Ackman, 1980; Sargent and Tacon, 1999). An increasing proportion of fish is being provided by aquaculture (Tidwell and Allan, 2002) but, paradoxically, diets have traditionally been based on fish meal and fish oil (FO) as the major finfish species farmed in Europe are carnivorous (Sargent and Tacon, 1999; Tacon, 2004). For a variety of reasons, the sustainable development of aquaculture requires that dietary FO must be replaced, with vegetable oils (VO) as the primary candidate alternatives (Barlow, 2000; Sargent et al., 2002; Pike, 2005). Salmonids, including Atlantic salmon (*Salmo salar* L.) and rainbow trout (*Oncorhynchus*

Abbreviations: BHT, butylated hydroxytoluene; FAF-BSA, fatty acid-free bovine serum albumin; EO, echium oil; FO, fish oil; HBSS, Hanks balanced salt solution; HUFA, highly unsaturated fatty acids (carbon chain length $\geq C_{20}$ with ≥ 3 double bonds).

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mykiss L.), can generally be grown on diets in which the FO has been replaced by VOs without compromising growth performance or significantly affecting fish health and welfare (Bell et al., 2001, 2002; Torstensen et al., 2000, 2006; Robin et al., 2003). However, this practice leads to increased C₁₈ PUFA and reduced *n*–3 HUFA in the flesh of the fish, potentially compromising the nutritional quality to consumers (Bell et al., 2001, 2002; Torstensen et al., 2000, 2006; Robin et al., 2003). Several studies have shown that feeding salmonid fish, including Arctic charr (*Salvelinus alpinus* L.), with VOs increased the activity of the hepatic HUFA biosynthesis pathway (Tocher et al., 2001, 2003; Zheng et al., 2005). However it is clear that the activity of this pathway is not sufficient to compensate for lack of dietary HUFA.

The mechanism underpinning an increased HUFA synthesis pathway in fish fed VO is not entirely clear. As HUFA such as arachidonic acid (ARA, 20:4*n*–6), eicosapentaenoic acid (EPA, 20:5*n*–3) and docosahexaenoic acid (DHA, 22:6*n*–3) are known to inhibit fatty acid desaturase activity (Brenner, 1981), possibly through suppressing gene expression (Tocher, 2003), it is assumed that the primary mechanism is increased gene expression of the fatty acid desaturases and/or elongases, as a consequence of reduced levels of dietary HUFA (Tocher, 2003). The role that increased fatty acid substrate provision (18:2*n*–6 or 18:3*n*–3) plays is less clear (Tocher et al., 2003). Early work determined that the rate limiting step, at least for the production of ARA from 18:2*n*–6 in mammals, was Δ6 desaturase activity (Brenner, 1981). By definition, this would dictate that the activity of the entire pathway would be determined by the activity of this, the first enzyme in the chain. Certainly, high levels of dietary 18:3*n*–3, supplied by linseed oil, did not alleviate the problem of reduced *n*–3HUFA in salmon fed high VO (Tocher et al., 2002; Bell et al., 2003, 2004). However, logic implies that the production of HUFA could be increased if the rate-limiting step in the HUFA synthetic pathway was bypassed. The seed oils of some plants, particularly of the Boraginaceae species, can be relatively rich in the Δ6 desaturated fatty acid, γ-linolenic acid (GLA, 18:3*n*–6), but seed oils rich in the *n*–3 homologue, stearidonic acid (STA, 18:4*n*–3) are less common (Padley et al., 1986; Moine et al., 1992). However, some Boraginaceae species can contain high levels of STA with up to 21% being reported in *Echium asperrimum* (Guil-Guerrero et al., 2001). Echium oil is thus similar to borage oil except that the levels of 18:4*n*–3 can exceed those of its *n*–6 series equivalent GLA.

In the present study, we aimed to test the hypothesis that feeding diets containing relatively high amounts of both Δ6 desaturated fatty acids, specifically STA and GLA, may be beneficial in salmonid culture. The rationale being that STA and GLA would be better PUFA substrates for HUFA synthesis in the fish as they do not require the activity of the reputed rate-limiting step enzyme, fatty acid Δ6 desaturase. In addition to determining basic growth performance parameters and tissue fatty acid compositions, the activity of the HUFA biosynthetic pathway in isolated hepatocytes was investigated to determine the effect a diet rich in Δ6 desaturated products had on this important pathway. Arctic charr were chosen for this trial as different populations or morphs with different feeding habits were available and these

have been reported previously to show differences in HUFA biosynthetic capacity (Tocher et al., 2001).

2. Materials and methods

2.1. Animals and diets

The Arctic charr (*S. alpinus* L.) investigated were from two populations held in the FRS Fish Cultivation Unit, Aultbea, and were originally obtained from two locations. One was from Loch Rannoch, Perthshire, which is deep and contains three distinct charr morphs including a demersal, piscivorous population (Rannoch charr), and the other population was from Loch Coulin, Wester Ross, a shallow loch containing a planktivorous morph (Coulin charr) (Tocher et al., 2001). Fish were distributed randomly into eight 1 m diameter circular fiberglass tanks of 500 L capacity at 30 fish per tank. The tanks were supplied with non-recirculated fresh water (average temperature, 5.0±2.4 °C, range 1.4–10.8 °C) at 5 L/min. After a two-week acclimatization period, each population of charr was fed two diets in duplicate for a period of 16 weeks. Diets were fish meal based containing 47% crude protein and 21% crude lipid and differed only in the added lipid component which was either Northern hemisphere fish oil (FO) or echium oil (EO). The diets were prepared from a 1.5 mm base extrusion (Ecostart 17/47, BioMar Ltd., Grangemouth, UK) that were top coated with either FO or EO. The diet formulations and analysed proximate compositions are shown in Table 1, and fatty acid compositions in Table 2. The fish were fed a fixed ration of 3% of biomass per day with the ration being adjusted following assessment of biomass by bulk weighing every 28 days. After 16 weeks, fish were individually weighed and six fish per dietary treatment (three per tank) were killed by a blow to the head and samples of liver and muscle collected for

Table 1
Formulations (g kg⁻¹) and proximate compositions (percentage of total diet) of experimental diets

	Fish oil	Echium oil
Fishmeal ^a	500	500
Soya meal ^b	100	100
Wheat ^c	200	200
Micronutrients ^d	14	14
Fish oil ^e	186	40
Echium oil ^f	–	146
Proximate composition		
Protein	47.5±0.2	47.3±0.1
Lipid	20.5±0.1	20.8±0.2
Ash	5.5±0.1	5.6±0.1
Moisture	8.7±0.1	8.6±0.1

Proximate compositions are means ± S.D. (n=3).

^a LT94, Norsemeal Ltd., London, UK.

^b HiPro, Grosvenor Grain, Perth, UK.

^c J.D. Martin, Tranent, UK.

^d Vitamins and minerals (BioMar AS, Brande, Denmark) provided at values in excess of the requirements for salmonid fish (NRC, 1993).

^e Northern hemisphere fish oil, BioMar Ltd., Grangemouth, UK.

^f Technology Crops International, Braintree, UK.

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