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ScienceDirect
Aquaculture 273 (2007) 298 – 311
Aquaculture
www.elsevier.com/locate/aqua-online

Parr–smolt transformation and dietary vegetable lipids affect intestinal nutrient uptake, barrier function and plasma cortisol levels in Atlantic salmon

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Abstract

For Atlantic salmon, the gastrointestinal tract is the site of food digestion and nutrient uptake, a regulatory site for ion and water balance as well as a barrier against invading pathogens. During the parr–smolt transformation and subsequent seawater (SW) transfer, major changes occur in the intestine. A global shortage of fish oils (FO) for feed production is estimated to appear within a few years, and vegetable oils (VO) are being considered as alternatives for FO in fish feed production. However, VO influences the fatty acid composition of the polar lipids of cell membranes in the intestine which can disturb intestinal functions. A VO-based diet during the parr–smolt transformation, which is a sensitive developmental period, may cause adverse effects. Therefore, Atlantic salmon parr were fed either sunflower oil (SO) or FO as the major lipid source during out-of-season light controlled parr–smolt transformation. At three time points gill Na^+,K^+-ATPase activity and plasma levels of cortisol and growth hormone were assessed. Intestinal epithelia were sampled for assessment of nutrient absorption and bacterial translocation using an Ussing chamber *in vitro* system. While both dietary groups showed plasma hormone profiles indicative of successful parr–smolt transformation, the SO-fed fish had consistently increased cortisol levels compared to the FO-fed fish. Translocation of pathogenic bacteria increased, probably due to disturbed barrier functions, during the parr–smolt transformation. However, the fish fed the SO-diet maintained a higher barrier function compared to FO-fed fish, an effect that may be beneficial to these fish. Nutrient uptake was less affected by smoltification. Fish fed the SO-diet had higher uptake rates of amino acids and free fatty acids during mid-smoltification than fish fed the FO-diet. The combined effects of barrier function and nutrient uptake may suggest a positive effect of including vegetable lipids in the diet during the parr–smolt transformation. However, the vegetable lipid diet also seemed to act as a stressor and elevated the basal cortisol levels, which may be of concern in the context of general fish health and welfare.

Keywords: Ussing chamber; Smoltification; Growth hormone; Osmoregulation; *Aeromonas salmonicida*; *Salmo salar*; Bacterial translocation; Intestine; Amino acid uptake; Fatty acid uptake

1. Introduction

The Atlantic salmon parr–smolt transformation is a complex process when the fish prepare for downstream migration and a marine life while still in fresh water (FW) (McCormick and Saunders, 1987). A fundamental physiological change which occurs during this developmental

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doi:10.1016/j.aquaculture.2007.10.012

period is the increased ability of the fish to osmoregulate in seawater (SW). Being a major organ for maintenance of water and ionic balance, the intestine needs to pre-adapt for its role in SW, i.e. to actively be able to absorb ions and water. During the parr–smolt transformation, the intestinal fluid transport increases (Veillette et al., 1995) due to increased Na^{+},K^{+}-ATPase activity and a slight increase in the epithelial paracellular permeability (Sundell et al., 2003). After adaptation to SW, drinking rate increases (Nielsen et al., 1999; Fuentes et al., 1996) and the intestinal Na^{+},K^{+}-ATPase activity is further increased concomitant with a decrease in paracellular permeability. This suggests a redirection of the water flow from a paracellular to a more transcellular pathway after a period in SW (Sundell et al., 2003). The increased strength of the physical intestinal barrier is likely to help restrict the passive passage of potentially hazardous substances, including pathogens, from the ingested water. The barrier against pathogens consists of several layers of defense mechanisms including, endogenous microbiota, mucus and antibody secretions, the epithelial immune system and the physical barrier consisting of the epithelial monolayer and the tight junctions (Jutfelt, 2006). Disturbances in any of these components can result in increased translocation of live pathogenic bacteria from the intestinal lumen to the systemic circulation (Berg, 1995). Thus, during the parr–smolt transformation and the period immediately after seawater transfer, the changes occurring in intestinal permeability may disturb the barrier function. This is supported by the fact that disease resistance is known to decrease during smoltification and for a short period after seawater transfer (Cipriano and Bullock, 2001).

In fish, as in other vertebrates, the gastrointestinal tract is also the site of food digestion and nutrient uptake, and the migration from FW to SW also includes diet changes. In the parr stage, the diet is mainly freshwater crustaceans and insects, while at sea, crustaceans and fish are the main prey (Bell et al., 1994). Thus, the limnic diet is rich in 18:2n-6(n-6) and 18:3(n-3) fatty acids compared with the marine diet which is rich in the longer chain highly unsaturated fatty acids (HUFA) such as 20:5(n-3) and 22:6(n-3) (Sargent et al., 1999). Pre-adaptative changes in both fatty acid metabolism and tissue fatty acid composition have been found to occur during the parr–smolt transformation. This includes an increase in fatty acid elongase and desaturase activity of isolated hepatocytes as well as increases in the ratio of C20 and C22:C18 and n-3:n-6 fatty acids in salmonid tissue (Tocher et al., 2000, 2004).

In salmon aquaculture, the main source for feed production is wild-caught fish, but there is a need for replacing this with more sustainable feed sources, such as vegetable lipids (Naylor et al., 2000). Fish oil can be replaced with vegetable oils without detrimental effects on fish growth and mortality (Hardy et al., 1987; Dosanjh et al., 1998; Bendiksen et al., 2003). However, the fatty acid profiles of vegetable lipids differ from that of fish oils, in a similar fashion as the natural diet in FW differs from that in SW, and these differences are to a large extent reflected in the fatty acid profiles of muscle and liver (Bell et al., 2001; Dosanjh et al., 1998; Tocher et al., 2000). As the first tissue exposed to, and utilizing, the diet is the gastrointestinal tract, the enterocyte cell membranes may be particularly prone to alterations in dietary lipid composition. Recent studies have found a change in the fatty acid composition of polar lipids of the intestinal mucosa in response to dietary vegetable lipids in both rainbow trout and Atlantic salmon (Olsen et al., 2003; Björnsson et al., 2004). Changes in the fatty acid composition can lead to a range of physiological changes such as altered membrane fluidity (Leray et al., 1984), changes in epithelial enzyme activities (Di Costanzo et al., 1983; Cahu et al., 2000) and decreased barrier function (Barton et al., 1992).

The aim of the present study was to investigate the effects of a SO-based diet, expected to alter the membrane lipid composition, on intestinal nutrient absorption and barrier function during the sensitive period of parr–smolt transformation.

2. Materials and methods

2.1. Fish and experimental design

In this study, Atlantic salmon were monitored through three samplings during out-of-season parr–smolt transformation. The experiment started at the Matre Aquaculture station, Matredal, Norway, using juvenile Atlantic salmon of the NLA-strain. The salmon were hatched in mid-January 2003, and reared under continuous light from first feeding (standard commercial diet; Nor-Aqua Innovation Ltd.) in late February. In August 2003, 900 Atlantic salmon parr with an average weight of 42 g were transferred into six 60 L fiber glass tanks supplied with aerated fresh water. The fish were allowed to acclimate for two weeks, during which they were fed a standard commercial diet (Nor-Aqua Innovation Ltd.), at 2% body weight per day, by automatic feeders. On September 15th, the fish (average weight 44 g) were divided into two groups (in triplicates) and the feeding of the two experimental diets was initiated (see below). At the same time, the fish were subjected to a transient, square-wave change in light regime, from continuous light (LL) to short day (12:12LD) for six weeks, and then back to LL for six more weeks. This photoperiod treatment has been proven successful in inducing out-of-season smoltification (Hansen, 1998; Björnsson et al., 2000; Sundell et al., 2003).