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Effects of plant proteins on postprandial, free plasma amino acid concentrations in rainbow trout (*Oncorhynchus mykiss*)

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ABSTRACT

Postprandial patterns in plasma free amino acid concentrations were investigated in juvenile rainbow trout (*Oncorhynchus mykiss*) fed either a fish meal based diet (FM) or a diet (VEG) where 59% of fish meal protein (corresponding to 46% of total dietary protein) was replaced by a matrix of plant proteins from wheat, peas, field beans, sunflower and soybean. Blood samples were obtained from the caudal vein of 7 fish in each dietary treatment group prior to feeding, as well as: 2, 4, 6, 8, 12, 24, 48 and 72 h after feeding (sampling 7 new fish at each time point), and plasma amino acid concentrations were subsequently measured by HPLC. Nutrient digestibility and ammonia excretion of the two experimental diets were measured in a parallel experiment using a modified Guelph setup. Results showed that the appearance of most amino acids (essential and non-essential) in the plasma was delayed in fish fed the VEG diet compared to those fed the FM diet. Essential and non-essential amino acids furthermore appeared more or less synchronously in the plasma in fish fed the FM diet, while the appearance was less synchronised in fish fed the VEG diet. Differences in plasma concentrations between the two dietary treatment groups correlated largely with the amino acid content of the two diets except for methionine, lysine and arginine, where the differences were more extreme than what would be expected from differences in dietary concentrations. The apparent protein digestibility coefficient was higher in the VEG diet than in the FM diet (93 *versus* 92%; *t*-test, $P<0.05$), supporting that protease inhibitors from plant protein ingredients were not the cause of the delay. The apparent digestibility coefficient of carbohydrates (calculated as nitrogen-free extract (NFE)) was much lower in the VEG than in the FM diet (51 *versus* 76%; *t*-test, $P<0.05$). Combined with a higher NFE content in the VEG diet, this meant that there was 2.7 times more indigestible NFE in the VEG than in the FM diet (6.1 *versus* 2.2 g 100^{-1} g feed). Such difference may suggest that the uptake of amino acids (AA) was affected by dietary carbohydrates. Total ammonia-nitrogen (TAN) excretion was slightly, but non-significantly, higher in VEG fed fish than in FM fed fish (59 *versus* 55 mg TAN g^{-1} digested protein; *t*-test, $P>0.05$). In conclusion, the study showed that amino acid uptake patterns are affected when replacing fish meal with plant based protein ingredients.

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1. Introduction

Fish meal is the preferred protein source in diets for carnivorous and omnivorous fish species because of its high nutritional value, and because it until recently has been the most cost-effective protein source available (Hardy, 2010). However, the global fish meal (and fish oil) supply is no longer able to meet the increasing demand from an expanding aquaculture industry, and together with increasing and variable fish meal prices, this has made it necessary for the aqua-feed sector to find alternative protein ingredients including plants (Gatlin et al., 2007; Hardy, 2010). Replacing fish meal with its high protein content, excellent amino acid (AA) profile, high nutrient digestibility, high palatability, adequate amounts of micronutrients, as well as a general lack of anti-nutrients (Gatlin et al., 2007; Kaushik and Seiliez, 2010; Krogdahl et al., 2010) is not straightforward, especially in feed for carnivorous fish like salmonids. A large number of studies have investigated the effects of replacing fish meal with various plant protein ingredients, and the most frequent finding is that it is fairly unproblematic to replace moderate parts of the fish meal (Borquez et al., 2011; Glencross et al., 2011; Pratoomyot et al., 2010; Torstensen et al., 2008; Yang et al., 2011). Complete replacement is usually not successful due to problems related to the factors mentioned above (Bendiksen et al., 2011; Borquez et al., 2011; Espe et al., 2006; Francis et al., 2001; Gatlin et al., 2007), although complete or almost complete replacement of the fish meal fraction has been shown to be feasible in a few cases (Kaushik et al., 1995; Kousoulaki et al., 2009; Rodehutscord et al., 1995; Watanabe et al., 1997).

High replacement ratios require that anti-nutrients and indigestible substances are efficiently removed from alternative protein ingredients to meet the high protein requirement of fish. Furthermore, it is

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necessary to ensure that the dietary AA profile is optimised, for example by adding crystalline AAs, and/or by combining several plant protein sources with different AA composition (Francis et al., 2001; Kaushik and Seiliez, 2010; Wilson, 2002). The latter is of particular importance in feed for organic fish, where supplementation with crystalline AAs is prohibited (EU, 2007; EU, 2009).

It is thus well known that certain AA requirements have to be met to obtain optimal growth. In addition, it is generally believed that free AAs derived from feed proteins and/or crystalline AAs should be present simultaneously in the plasma at balanced ratios, and at the site of protein synthesis, in order to achieve efficient utilisation (Berge et al., 1994; Dabrowski and Guderley, 2002; Murai et al., 1982; Yamamoto et al., 1998). If this is indeed the case, it suggests that the timing by which AAs from different protein sources appear in the blood stream after a meal, and not just the overall dietary AA profile *per se*, is important for efficient utilisation of AAs. Furthermore, in mammals, protein retention efficiency has been shown to be affected by the feed protein source due to differences in absorption kinetics (Boirie et al., 1997; Bos et al., 2003; Deutz et al., 1998; Fouillet et al., 2002). This may similarly apply to fish given that they possess many of the same regulatory pathways (Cleveland and Evenhuis, 2010; Lansard et al., 2009; Lansard et al., 2010; Seiliez et al., 2008a,b; Seiliez et al., 2010; Skiba-Cassy et al., 2009).

Postprandial changes in plasma free AA concentrations have been investigated in several studies, most of which have compared diets containing a large proportion of crystalline AAs with diets containing either intact protein such as casein (Murai et al., 1987; Plakas et al., 1980; Yamada et al., 1981), or wheat gluten (Schuhmacher et al., 1997). Others have investigated the effect of adding crystalline AAs to a practical diet (Aoki et al., 2001; Tantikitti and March, 1995). In general, these studies have demonstrated that crystalline AAs appear faster in the plasma compared to AAs derived from the digestion of intact proteins. Reduced growth has been reported for salmonids fed diets containing large amounts of free AAs as compared to diets containing intact protein with an identical AA profile (Espe and Lied, 1994; Stone et al., 1989; Walton et al., 1986). Furthermore, reduced growth accompanied by elevated ammonia excretion has been demonstrated in turbot (*Scophthalmus maximus*) fed a diet where 56% of the fish meal was replaced with crystalline AAs (Peres and Oliva-Teles, 2005), indicating that crystalline AAs are oxidised to a larger extent than AAs originating from intact proteins.

To our knowledge, only one previous study has examined the postprandial time course of plasma AA concentrations in fish fed a diet with plant protein as the sole dietary protein ingredient (Yamamoto et al., 1998). According to this study, the peak level of plasma AAs occurred about 9 h later in rainbow trout (*Oncorhynchus mykiss*) fed diets based on total replacement of fish meal with either defatted soybean meal or malt protein flour, compared to fish fed a fish meal based diet. The authors suggested that the delay was related to differences in digestive processes in the gastrointestinal tracts, and to the speed by which feed was evacuated from the stomach. Elevated ammonia excretion in fish fed plant based diets compared to fish meal diets has been observed in some studies (Bonaldo et al., 2011; Kaushik et al., 2004; Lund et al., 2011; Robaina et al., 1995), suggesting a possible negative effect on protein utilisation. However, a direct link between "sub-optimal" timing in post-prandial AA uptake from plant protein and elevated ammonia excretion has not been reported.

The overall purpose of the present study was to explore if plant protein ingredients affect AA uptake patterns and concurrent nutrient utilisation in juvenile rainbow trout (*O. mykiss*), potentially contributing to explaining the limited success of replacing large amounts of fish meal with plant protein ingredients in feed for carnivorous fish. The specific objectives of the study were to examine: 1) if and how postprandial, plasma free AA concentration patterns in juvenile rainbow trout fed a diet with high inclusion of plant protein ingredients differed from plasma free AA patterns in fish fed a fish meal diet; and 2) if the high plant protein inclusion level affected nutrient digestibility and ammonia excretion.

2. Materials and methods

2.1. Fish

Juvenile rainbow trout of approximately 50 g were obtained from a local trout farm (Funderholme Fish Farm, Silkeborg, Denmark), and transported to the research facilities of the Technical University of Denmark at the North Sea Research Centre in Hirtshals. Two parallel experiments were carried out following a 3 week quarantine period: one experiment investigating postprandial changes in plasma amino acid concentrations; and one experiment determining nutrient digestibility and ammonia excretion with growth and feed conversion ratios also being monitored.

2.2. Diets

A fish meal based diet (FM) and a diet (VEG) where 59% of the fish meal protein (corresponding to 46% of total dietary protein) was replaced by a matrix of plant proteins, were formulated and prepared by BioMar Ltd, Denmark (Table 1). The diets were formulated to be iso-energetic and iso-nitrogenous, and the plant protein matrix was formulated to meet the expected essential AA requirement of the fish. The content of crude protein, crude fat, total phosphorus, dry matter (DM), nitrogen-free extract (NFE) and ash in the diets was determined as described in Dalsgaard et al. (2009) (Table 1), and the AA composition of the two diets was determined as described in section 2.5.

2.3. Nutrient digestibility, ammonia excretion, and fish growth

A total of ninety fish with an initial mean weight of 101 ± 9 g (mean $\pm$ SD) were distributed among six (i.e. stocking density of 15 fish tank^{-1}), 189 L, flow-through thermoplastic tanks modelled as a modified Guelph digestibility system (Dalsgaard and Pedersen, 2011). The fish were acclimatised to the experimental facility and fed the experimental diets for 10 days prior to the start of the experiment, feeding the two diets to triplicate tanks randomly distributed among the six tanks. A digestibility study was subsequently performed as described in Dalsgaard and Pedersen (2011), feeding each diet for 9 days at a daily feeding ration of 1.6% of the estimated biomass in each tank. All feed consumed in each tank during the study was accounted for, and all faeces produced was collected. The first three faecal sampling days served as an extra acclimatisation period, while samples from each of the three consecutive days were pooled, yielding two pooled faecal sampling periods for calculation of apparent digestibility coefficients. The apparent digestibility coefficient (ADC) of macronutrients was subsequently calculated using the direct method (Jobling, 1994, 2001), which requires knowledge of both the total amount of feed consumed and collection of all the faeces produced, using the equation:

$$ADC_i = (C_i - F_i)/C_i,$$

where i = protein, lipid, NFE or DM, C = consumed amount of i, and F = faecal loss of i.

The fish were anaesthetised using phenoxy-ethanol and weighed at the start (day 0) and at the end (day 10) of the digestibility study. The specific growth rate (SGR,% day^{-1}) was calculated based on the biomass gained in the tanks using the equation by Hopkins (1992):

$$SGR = Ln(W(t_i)/W(t_0))/(t_i - t_0)x100,$$

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