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Aerobic exercise increases the utilization efficiency of energy and protein for growth in Atlantic salmon post-smolts

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ABSTRACT

Aerobic exercise training may improve growth and help to protect fish from viral and bacterial diseases. This study was conducted to determine the effect of increased sustained aerobic exercise on the maintenance requirements and the efficiency of utilization of digestible protein (DP), digestible amino acids and metabolizable energy (ME) for growth above maintenance of Atlantic salmon post-smolts. The fish were held in tanks with currents of 7 (low speed) or 23 (high speed) cm s^{-1} (initial speeds 0.32 and 1.06 body lengths s^{-1}) for 62 days and fed a fishmeal-based diet in excess or at levels approximating 30, 40, 60 and 80% of the intake of the full-fed groups. In the full-fed groups, there was no significant effect of exercise treatment on feed intake, final weights, growth rates, feed efficiency or whole-body composition. An extrapolation to zero weight gain showed that the increased speed resulted in an increase in the maintenance requirement from 5.3 to 13.4 g dry matter $fish^{-1}$. The maintenance requirement for ME, which includes the energy used for activity, was 46.5 kJ $kg^{-0.8}$ d^{-1} in the high exercise groups and 24.7 kJ $kg^{-0.8}$ d^{-1} in the low exercise groups. Our calculations showed that true maintenance, in which energy used for activity has been removed, was 15.3 kJ $kg^{-0.8}$ d^{-1} at zero speed. Above maintenance, the efficiency of utilization of ME for energy gain was 0.89 in the high exercise groups and 0.70 in the low exercise groups ($P < 0.05$). The maintenance requirements for DP were three times higher in the high exercise groups than in the low speed groups, but above maintenance, DP was used more efficiently for protein gain in the high exercise groups (0.70) than in the slow groups (0.60) ($P < 0.05$). The efficiency of utilization of digestible arginine, histidine, isoleucine, leucine, lysine and phenylalanine for gain of these amino acids above maintenance tended to be greater in the salmon exercised at the high speed compared with those exercised at the low speed ($P \leq 0.1$). The maintenance requirements for most of the digestible amino acids were about twice as high in the high speed groups compared with the low speed groups. These results show that with increased aerobic exercise, the higher activity costs of Atlantic salmon are associated with increased utilization of nutrients and energy for growth.

1. Introduction

Interest is growing for using aerobic endurance training to improve growth and reduce stress in fish farming. Increased growth rates may be obtained in salmonids that are exercised (Castro et al., 2011, 2013b; Christiansen et al., 1989; Davison and Goldspink, 1977; East and Magnan, 1987; Jørgensen and Jobling, 1993, 1994; Leon, 1986), but limitations seem to exist when speeds over about 1.5 body lengths (bl) s^{-1} are used. The exception to this seems to be with Arctic charr (*Salvelinus alpinus* L.) where higher growth rates were found at 2.0 bl s^{-1} compared with lower speeds (Christiansen and Jobling, 1990). Feed efficiency may be improved at these moderate speeds, but not always (reviewed by Jobling et al., 1993; Castro et al., 2011, 2013b).

Protein and energy requirements for maintenance and for growth above maintenance have been estimated in fish during the last three decades using the comparative slaughter technique and different ration levels (Huisman, 1976; Lupatsch et al., 1998; Meyer-Burgdorff et al., 1989). This method has been expanded to include requirements for amino acids (Grisdale-Helland et al., 2011a,b; Hauler and Carter, 2001; Hauler et al., 2007; Helland et al., 2010). The efficiency of digestible protein (DP) utilization for growth above maintenance (k_{DP}) may be influenced by fish species, diet ingredients and composition, and feed production technique (Glencross, 2008; Glencross et al., 2007, 2008; Hatlen et al., 2007; Helland et al., 2010; Lupatsch et al., 1998, 2001b). Species and feed production technique also affect the efficiency of digestible energy (DE) utilization for growth above maintenance (k_{DE}); whereas dietary ingredients or chemical composition has not been shown to affect this efficiency measure (Glencross et al., 2007, 2008; Grisdale-Helland et al., 2011a; Hatlen et al., 2007; Lupatsch et al., 2001b). Temperature and hypoxia have not been found to affect either k_{DP} or k_{DE} (Azevedo et al., 1998; Glencross, 2009; Lupatsch and Kissil, 2005; Lupatsch et al., 2001a; Pirozzi et al., 2010). In this model, energy used for activity is included in the estimate of maintenance.

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The effect of exercise on maintenance levels and the efficiency of utilization of these nutrients and energy have not been reported.

Lipid seems to be the major fuel of aerobic exercise in fish, with carbohydrate and protein being utilized at lower levels (Kieffer et al., 1998; Kutty, 1968, 1978). Acyl-CoA oxidase (ACO) and carnitine palmitoyltransferase 1 (CPT1) are required for β-oxidation of long-chain fatty acids in peroxisomes and mitochondria. Glutamate dehydrogenase (GDH) regulates oxidative deamination of glutamic acid and, since this reaction is reversible, amino acids may also be synthesized. In Atlantic salmon, GDH is encoded by three transcripts, but no literature is available about the effects of these three genes on amino acid and energy metabolism in this species. The objective of the present trial was to compare the requirements for energy, protein and amino acids for maintenance and growth above maintenance, and the transcription levels of ACO, CPT1 and GDH, in Atlantic salmon post-smolts exposed to two levels of continuous, moderate aerobic exercise that might be practical for fish farming conditions.

2. Materials and methods

2.1. Diet

An extruded diet (2.5-mm pellets) based on fish meal was produced by Nofima AS (Fyllingsdalen, Norway) (Table 1). Yttrium oxide was included in the diets as an inert marker for digestibility determinations. The diet was analyzed for dry matter (DM) (105 °C, until constant weight), crude lipid (Soxtec HT6 after hydrolysis with HCl, Tecator, Höganäs, Sweden), nitrogen (crude protein (CP) = N × 6.25; Kjeltec Auto System, Tecator, Höganäs, Sweden) and ash (550 °C, overnight). Gross energy was measured using an adiabatic bomb calorimeter (Parr 6300, Parr Instrument Company, Moline, IL, USA). Yttrium was analyzed by inductivity-coupled plasma mass-spectroscopy (ICP) at Eurofins (Moss, Norway). The amino acids in the diet were analyzed using a Biochrom 30 amino acid analyzer (Cambridge, U.K.) following the EC Commission Directive 98/64/EC (1999), after hydrolysis in 6 N HCl for 23 h at 110 °C. Tryptophan and tyrosine were analyzed after basic hydrolysis (Hugli and Moore, 1972). All amino acid concentrations in this paper are presented in their anhydrous, protein-bound forms, unless otherwise indicated.

Table 1
Formulation and composition of the experimental diet.

Ingredients (g kg^{-1})	
Fish meal[a]	506.4
Fish oil[b]	193.1
Wheat starch	135.1
Wheat gluten	94.8
Krill meal	30.0
Vitamin premix[c]	20.0
L-Lysine HCl[d]	15.0
Tryptophan[d]	1.2
Mineral premix[c]	4.0
Carophyll® Pink (10%)[e]	0.25
Yttrium oxide	0.10
Composition (g or MJ kg^{-1})	
Dry matter (DM)	952.5
In DM	
Crude protein	489.5
Sum amino acids[f]	328.3
Crude lipid	283.7
Ash	76.6
Yttrium	0.1
Gross energy	25.0
Amino acids[f]	
Ala	18.0
Arg	23.8
Asx[g]	26.0
Cys	3.5
Glx[g]	59.9
Gly	18.3
His	7.2
Ile	14.2
Leu	25.0
Lys	30.5
Met	9.1
Phe	15.0
Pro	18.4
Ser	14.4
Thr	13.0
Trp	4.1
Tyr	11.3
Val	16.4

[a] 30% capelin, 10% blue whiting, 60% capelin waste.
[b] NorSalmOil, Norsildmel, Norway.
[c] As described by Mundheim et al. (2004).
[d] Donated by Ajinomoto Eurolysine S.A.S., Paris, France.
[e] F. Hoffman-La Roche Ltd., Basel, Switzerland.
[f] Protein-bound form.
[g] Asx represents aspartate and aspargine and Glx represents glutamate and glutamine.

2.2. Growth trial

In December 2009, seven weeks after transfer to seawater, groups of 26 2-day fasted Atlantic salmon (*Salmo salar*) post-smolts (initial weights 116.8 ± 0.4 g, mean ± S.D., N = 18 tanks) were randomly allocated to 18 cylindro-conical tanks (500 L; 82 cm diameter) at Nofima, Sunndalsøra. The tanks were supplied with seawater (11.0 ± 0.3 °C, 32.5 ± 0.2 g L^{-1} salinity) at a flow rate of 12 L min^{-1} (24 h light). The center of each tank was fitted with a plastic pipe (31.5 cm diameter) which reduced the area in the tank with lowest water speed. A wire mesh fence was attached between the pipe and the edge of the tank to prevent the fish from drifting back over. A frequency-controlled pump (Hanning Elektro Werke, PS 18-300; Oerlinghausen, Germany) was attached to each tank and directed the water current. Water was pumped from the middle of the tanks and returned through an inlet pipe with closed ends and side nozzles. The water speeds were calibrated by using the average speed measured at twelve points (four horizontal locations and three depths at each location (Höntzsch HFA propeller, Waiblingen, Germany with HLOG software)). The water velocities were 7 and 23 cm s^{-1} and since the initial fish lengths (N = 40 individuals) were 21.6 ± 0.7 cm, the initial swimming speeds were 0.32 and 1.06 bl s^{-1}. The water current was kept constant during the trial and consequently the relative swimming speeds decreased as the fish grew. Unfortunately, the final lengths of the fish were not measured; these have been estimated using the data from the study of Helland et al. (2010) where Atlantic salmon with the same physiological stage were used ($y = 15.81 + 0.063x - 0.00007x^2$, where y is weight (g) and x is length (cm), $R^2 = 0.97$, N = 415). By the end of the trial, the estimated relative speeds ranged from 0.25 to 0.29 and from 0.93 to 0.97 bl s^{-1} in the low and high speed treatments, respectively.

The effluent water of each tank was led into a wire mesh box to enable sieving of waste feed. In order to minimize leaching of the waste feed, the effluent water was directed to two different areas of the wire box using pinch valves on the water pipes, dependent on whether feeding was occurring. Oxygen saturation was measured daily and was maintained over 85% with oxygen supplementation (Thorarensen and Farrell, 2011). Water temperature and salinity were also measured daily.

The fish were fed for 60 days from automatic feeders, once per hour. For each exercise treatment, duplicate groups were fed in excess to estimate maximum intake and duplicate groups were fed at levels approximating 30, 40 and 80% of the intake of the full-fed groups. In addition, single tanks for each treatment were fed at 60% of the full-fed ration level. The waste feed was collected daily, weighed and stored frozen. Taking into account the waste feed level and the percentage recovery of DM from the diet (Helland et al., 1996), the approximate intake of fish in each tank was calculated. The feeding level of each