Effect of feeding rate on nutrient digestibility in Atlantic salmon, *Salmo salar* L.

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Abstract: A digestibility trial was conducted to examine the effect of feeding rate on dry matter, gross energy, crude protein and phosphorus digestibility in Atlantic salmon (*Salmo salar*). Duplicate groups of fish were fed 0.25, 0.5, 0.75, 1.0, 1.25 and 1.9% BW/day. The faeces were collected by Guelph-type collectors for five successive days. Dry matter, protein and phosphorus digestibilities were all significantly ($P<0.05$) affected by feeding rate. Dry matter digestibility was significantly lower in fish fed 0.25% BW day in comparison with fish fed 0.5, 0.75 and 1% BW day. Protein digestibility was significantly lower in fish fed 0.25% BW/day in comparison with 1.25% BW day. Phosphorus digestibility was significantly lower in fish fed 0.25% BW/day in comparison with all other treatments except for 1% BW day. There were no significant differences for energy digestibility between fish fed with different amount of feed. The main effect was reduced digestibility at the lowest level of intake with no obvious relationship between feeding rate and digestibility above this amount. This was explained by a relatively higher loss of endogenous faecal nitrogen and phosphorus at sub-maintenance feeding.

Keywords: Atlantic salmon, Phosphorus digestibility, Feeding rate, Apparent digestibility

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Introduction

Considerable information is available on nutritional effects on digestibility particularly in relation to nutrient and ingredient composition (Bureau *et al.,* 1999; Engin & Carter, 2002; Euesbio *et al.,* 2004; Glencross *et al.,* 2004; Tibbetts *et al.,* 2004; Koprucu & Ozdemir, 2005). Furthermore, biological and environmental factors affect nutrient digestibility, but their effects are not well defined and results are contradictory (De Silva & Anderson, 1995; Fernández *et al.,* 1998; Bureau *et al.,* 2002). Biological factors such as animal size and age or environmental factors such as temperature and salinity may also affect the digestibility (Jobling, 1993, 1994,1996; De Silva & Anderson, 1995; Guillaume and Choubert, 2001; Bureau *et al.,* 2002). Studies on the effect of feeding rate on nutrient digestibility in fish are limited (Windell *et al.,* 1978; Henken *et al.,* 1985; Cho & Kaushik, 1990; Cui *et al.,* 1994; Yamamoto *et al.,* 2001) and sometimes controversial (Fernández *et al.,* 1998).

Digestibility is generally assumed independent of ingestion rate (Guillaume *et al.,* 2001). Feed intake did not affect dry matter, gross energy, crude protein, lipid or phosphorus apparent digestibility (Cho & Kaushik, 1990; Fernández *et al.,* 1998). However, some studies have shown that feeding rate influenced nutrient digestibility (Windell *et al.,* 1978). Rainbow trout fed the highest amount of feed had significantly lower digestibility for dry matter, energy and carbohydrate but not for protein and lipid digestibility (Windell *et al.,* 1978). Apparent digestibility of dry matter, energy, protein or lipid decreased with increasing feeding rate (Henken *et al.,* 1985; Yamamoto *et al.,* 2001). In contrast, Cui *et al.* (1996) found higher energy digestibility at the highest feed intake and they did not find differences among other intake levels. In the present study, fish fed for a short period of time to confirm that the fish are growing and responding correctly to the amount of feed or not.

The purpose of this study was to investigate the effect of feeding rate on nutrient digestibility and specially phosphorus digestibility in Atlantic salmon. Six intake levels were selected from below maintenance to slightly greater than satiation level.

Materials and methods

The diet was formulated to contain 48% crude protein, 22.5MJ/kg gross energy and 0.7% total phosphorus (Table 1). All nutrient requirements of Atlantic salmon were provided based on values for salmonids (NRC 1993). Phosphorus concentration was set at the requirement level (0.7%). South American fish meal (Skretting, Cambridge, Tasmania, Australia), blood meal (Skretting, Cambridge, Tasmania, Australia), and casein (New Zealand Dairy Board, Wellington, New Zealand) were used as protein sources in the diet. Dietary ingredients were mixed using a Hobart mixer, pelleted with a laboratory pelletizer (California Laboratory Pellet Mill) and the pellets dried at 30°C for 24h. The diets were refrigerated at 4°C until use.

The experiment was performed at the School of Aquaculture, University of Tasmania. Atlantic salmon, *Salmo salar* L. were obtained from Wayatinah Salmon Hatchery (SALTAS, Tasmania, Australia) and transferred to the Aquaculture Centre, School of Aquaculture. Fish were kept in 300-L circular tanks in a recirculation system where water quality was maintained through physical and biological filters (Sajjadi & Carter, 2004a). Fish were maintained on a commercial feed (3mm Salmon, Skretting, Cambridge, Tasmania, Australia) for seven days. Water replacement rate in the system was about 20% /day and water flow through the tanks was 8-10L/min. Oxygen concentration was 90.0±0.7% of saturation, average water temperature was 14.9±0.8°C and a natural photoperiod (approximately, 9L:15D) was in effect over the trial. The trial was carried out in freshwater.

After the acclimation period, the fish were fed to satiation twice daily at 0900 and 16;00h with the experimental diet for ten days and feed intake was determined for two successive days and the data used to set the amount of feed for the experiment. Satiation was judged to have been reached when approximately 20 pellets were not eaten and lost via the outlet water. Uneaten pellets were collected by a mesh collector placed in the outlet water (Helland *et al.,* 1996) and feed intake calculated by subtracting the number of uneaten from supplied pellets. At the beginning of experiment, fish were anaesthetised in benzocaine (50mg/L) and the wet weight of individual fish measured (Sajjadi & Carter, 2004a). Twenty fish

(156.4±0.20g) were kept in each tank. Amount of feed were set at 0.25, 0.5, 0.75, 1.0, 1.25 and 1.9% BW day. Duplicate groups of fish were fed each ration twice daily at 09:00 and 16:00h by automatic feeders.

Feed efficiency ratio (FER) was calculated as:

FER (g/g DM) = total weight gain (g wet weight) / total feed intake (g DM)

At the end of 10 day experiment, the fish were fasted for 24 h and the wet weight measured for individual fish.

Apparent digestibility (AD) was measured over five successive days. Ytterbium oxide [Sigma Chemical Co., NSW, Australia] (1g.kg diet) was added to the diets as an inert marker (Sugiura *et al.,* 1998). The fish were fed the diets containing ytterbium oxide for nine days and on days 5, 6, 7, 8 and 9 faecal samples were collected by Guelph-type settlement collectors (Carter & Hauler, 2000). One hour after feeding at 16:00h, the collectors were washed of uneaten food and faeces collected from that time until 1 hour before next feeding time (0900 h). Faeces were frozen and then freeze-dried and used for the analysis of ytterbium oxide and nutrients (see below). The faecal samples from the five collection days were pooled in equal weights for each tank and frozen at –20°C until analysis. AD was calculated according to Maynard and Loosli (1969):

AD (%) = 100 – [100 (% I diet / % I faeces) × (% N faeces / %N diet)]

Where I is the inert marker and N is the nutrient.

Chemical analysis of diets and faeces were performed according to standard methods: dry matter (freeze dry to constant weight); ash (AOAC, 1995); crude fat (Bligh and Dyer, 1959); protein (Kjeldahl using a selenium catalyst [N × 6.25]) and energy (bomb calorimeter: Gallenkamp Autobomb, calibrated with benzoic acid). For analysis of the ytterbium marker in diets and faeces, 5 ml of HNO_3 was added to 100 mg samples in digestion tubes and boiled. After cooling, the samples were diluted to 10 ml with distilled water and ytterbium content of diets and faeces measured by flame atomic absorption. Phosphorus in the diet and faeces were analysed by the molybdovanadate method (AOAC, 1995).

Mean values are reported ±Standard Error of the Mean (S.E.M). Comparison between means was by one-way ANOVA after confirming the normality and homogeneity of variance (SPSS, version 11.5). Multiple comparison was by Tukey.

Differences were considered significant at $P<0.05$. The relationship between feeding rate-growth and feeding rate-FER were modelled using regression analysis, and best-fit curve was chosen according to its estimated reliability with checking R-square value (Microsoft Excel, 2000). Correlation matrices of nutrient digestibility were compared by Pearson correlation coefficient (SPSS, version 11.5).

Table 1: Ingredient and chemical composition of experimental diet

		Diet
Ingredient composition (g.kg)	Casein	272
	Fish meal	200
	Blood meal	110
	Pre-gelatinized starch	150
	Fish oil	165
	Alpha cellulose	50
	Bentonite	32
	Carboxymethyl cellulose	10
	Mineral mix[1]	3
	Vitamin mix[2]	3
	Choline chloride	1
	Stay C[3]	3
	Ytterbium oxide	1
Chemical composition (g.kg DM)	Dry matter (g.kg)	955
	Crude protein	480
	Crude fat	216
	Ash	73
	Gross energy (MJ.kg DM)	22.42
	Total Phosphorus (g.kg DM)	7.8

1- Supplied (mg/kg diet): 70, $CuSO_4$ $5H_2O$; 1089.3, $FeSO_4$ $7H_2O$; 184.5, $MnSO_4 H_2O$; 1.98, Na_2 SeO_3; 395.82, $ZnSO_4$ $7H_2O$; 4.32, KI; 28.62, Co SO_4 $7H_2O$.

2- Supplied (mg/kg diet): 15.0, Vitamin A acetate; 18.0, Vitamin D_3 powder; 300, Rovimix E50; 6.0, Menadione sodium bisulphate; 12.0, Riboflavin; 65.22, Calcium D-pantothenate; 30.0, Nicotinic acid; 0.03, Vitamin B12; 0.45, d-Biotin; 3.00, Folic acid; 3.37, Thiamin HCl; 10.98, Pyridoxine HCl; 900, Myo-inositol.

3- L-Ascorbyl-2-polyphosphate (Roche Vitamins Australia Ltd, Sydney, Australia).

Results

Initial feed intake was 1.7% BW/day, so feeding rates were selected across a broad range from below maintenance (0.25% BW day) to slightly greater than satiation (1.9% BW day). Weight gain was negative in fish fed 0.25% BW day and significantly ($P<0.05$) lower than fish fed 1.0, 1.25 and 1.9% BW day (Table 2). Growth was positive at 0.5% BW day and the relationship between feeding rate and growth was curvilinear (Fig. 1). FER was negative in fish fed 0.25% BW day and significantly lower than fish fed at any of the other amount of feed (Table 2). Feeding rate-FER relationship was curvilinear and FER peaked at the range of 1.25-1.5% BW day and then decreased (Fig. 2).

Feeding rate had no significant effect on apparent digestibility for gross energy (Table 3). The apparent digestibility for phosphorus, dry matter and protein between fish fed different amount of feed were significantly different (Table 3). A 0.5% BW day feeding rate was approximately the maintenance feeding rate for these fish. Fish fed 0.5% BW day had significantly higher dry matter digestibility in comparison with 0.25, 1.25 and 1.9% BW day. Apparent digestibility for dry matter was lower for fish fed 0.25% in comparison with fish fed 0.5, 0.75 and 1% BW day. There were no significant differences in dry matter digestibility between fish fed 0.25, 1.25 and 1.9% BW day. There was neither significant difference in dry matter digestibility for fish fed 0.75, 1, 1.25 and 1.9% BW day nor between 0.5, 0.75 and 1% BW day (Table 3). Protein digestibility was lower for fish fed 0.25% BW day in comparison with fish fed 1.25% BW day. There were no significant differences between other treatments for protein digestibility. Phosphorus digestibility was lower in fish fed 0.25% BW day in comparison with 0.5, 0.75, 1.25 and 1.9% BW day. There were no significant differences in phosphorus digestibility between fish fed 0.25 and 1% BW day and no significant differences between 1% BW day and other treatments.

Correlation matrix of nutrient digestibility has been shown in Table 4. The highest correlation was found between crude protein digestibility and phosphorus digestibility (r=0.82). There were significant correlation between crude protein and dry matter digestibility (r=0.72) and between phosphorus and dry matter digestibility (r=0.79) ($P<0.01$).

Table 2: The growth performance of Atlantic salmon fed different amount of feed (mean ± S.E.M, n=2)

Parameter	Unit	Feeding rate (%BW day)						
		0.25	0.5	0.75	1.00	1.25	1.9	P
Initial weight	(g)	156.3 ± 0.05	156.6 ± 0.35	156.5 ± 0.25	156.4 ± 0.10	156.5 ± 0.30	156.2 ± 0.20	ns
Final weight	(g)	152.2 ± 1.00[a]	157.2 ± 0.35[ab]	163.0 ± 0.15[b]	167.5 ± 1.00[bc]	175.1 ± 0.15[cd]	180.3 ± 4.40[d]	< 0.05
Weight gain	(g)	-4.03 ± 0.94[a]	0.64 ± 0.05[ab]	6.51 ± 0.12[ab]	11.13 ± 1.09[bc]	18.52 ± 0.46[cd]	24.10 ± 4.63[d]	< 0.05
FER	(g/g DM)	-1.29 ± 0.30[a]	0.10 ± 0.01[b]	0.68 ± 0.01[bc]	0.84 ± 0.08[bc]	1.09 ± 0.02[c]	0.93 ± 0.15[c]	< 0.05
Survival	(%)	100	100	100	100	100	100	ns

Means with same letter are not significantly different (Tukey multiple comparison).

*** no significant**

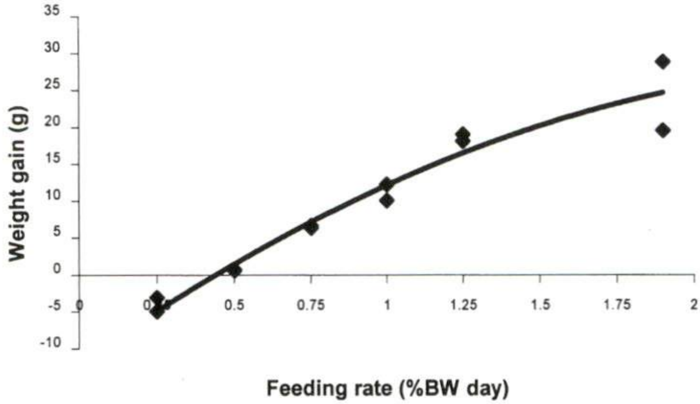

Figure 1: The relationship between feeding rate and weight gain in Atlantic salmon ($y=-5.413x^2+29.497x-11.94$; $r^2=0.95$)

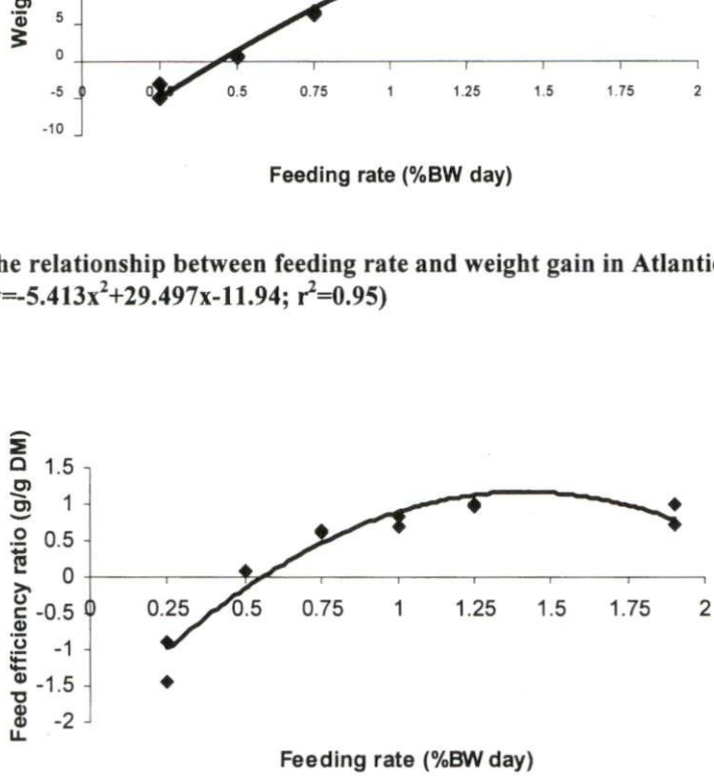

Figure 2: The relationship between feeding rate and feed efficiency ratio in Atlantic salmon ($y=-1.5918x^2+4.4992x-2.009$; $r^2=0.92$)

Table 3: Apparent digestibility (AD) (%) for dry matter (DM), energy (kJ), crude protein (CP) and phosphorus (P) in Atlantic salmon fed different amount of feed (mean ± S.E.M, n=2)

Parameter	Unit	Feeding rate (%BW day)						
		0.25	0.50	0.75	1.00	1.25	1.90	P
AD_{DM}	(%)	79.51 ± 0.12[a]	82.94 ± 0.59[c]	89.10 ± 0.04[bc]	81.43 ± 0.46[bc]	80.91 ± 0.01[ab]	80.92 ± 0.06[ab]	< 0.05
AD_{KJ}	(%)	88.56 ± 0.79	89.58 ± 1.30	89.65 ± 0.32	88.63 ± 0.63	89.02 ± 0.75	88.69 ± 0.87	ns
AD_{CP}	(%)	92.77 ± 0.08 [a]	94.79 ± 0.75[ab]	94.87 ± 0.37[ab]	97.84 ± 0.36[ab]	95.10 ± 0.04[b]	94.74 ± 0.22[ab]	< 0.05
AD_{P}	(%)	39.81 ± 1.49[a]	55.88 ± 3.75[b]	52.28 ± 1.13[b]	49.76 ± 0.44[ab]	51.30 ± 1.02[b]	54.79 ± 0.47[b]	< 0.05

Means with same letter are not significantly different (Tukey multiple comparison).

*** no significant**

Table 4: Correlation (r) matrix of nutrient digestibility in Atlantic salmon (n=12)

AD	AD[1]			
	DM[2]	KJ[3]	CP[4]	P[5]
KJ	0.54	-------	--------	--------
CP	0.72*	0.47	--------	--------
P	0.79*	0.41	0.83*	--------

***Correlation significant at P<0.01 (selected to reduce probability of type I error).**

1- Apparent digestibility

2- Dry matter

3- Energy

4- Crude protein

5- Phosphorus

Discussion

The diet used here had previously been shown to promote growth for Atlantic salmon; when they were fed to satiation, the SGR and FER were 1.30 and 1.22, respectively (Table 1) (Sajjadi & Carter, 2004b). Generally, growth trials are conducted for 8-12 weeks, depending on fish size and growth rate. In the present study, despite the short length of the experiment, there were significant differences in growth and FER between different treatments (Table 2). It is important to note that the strong relationship between feeding rate and growth confirmed that the AD values were generated from salmon of the appropriate nutritional status (Fig. 1). The strong feeding rate-growth relationship showed that the salmon had clearly acclimated to the experimental conditions. The fish fed 0.25% BW day had a negative growth rate and feed efficiency ratio (FER) (Fig. 2). Regression relationships between feeding rate-growth and feeding rate-FER were typical (Jobling, 1994) as would be expected. In most fish, the relationship between feeding rate and wet weight growth is non-linear (Brett and Groves, 1979; Carter *et al.,* 2001), but linear relationships were observed in some studies (Cui *et al.,* 1994, 1996). In the present study, with increasing level of feed intake, growth increased and reached a plateau at the highest feeding rate (in excess). Maintenance feeding rate was about 0.5% BW day. FER increased with increasing level of feed intake and reached to a plateau and then decreased. This was in agreement with other studies, when feeding rates were selected from below maintenance to slightly greater than satiation level and a typical graph of FER- feeding rate was observed (Halver, 1989; Storebakken *et al.,* 1991; Jobling, 1994; Mihelakakis, 2001; Bureau *et al.,* 2006). As the optimum feeding rate is the highest point in FER-feeding rate graph, when optimum feeding rate is not given to fish, the graph does not reach to plateau (Jobling, 1994).

Feeding rate influenced nutrient digestibility in the present study, but only in a minor way and there were no clear trends with increasing feeding rate (Table 3). The fish fed 0.25% BW day had lowest digestibility values for protein, dry matter and phosphorus in the present study. Feeding rate had no effect on energy digestibility. Feeding rate level had no significant effect on apparent protein digestibility (Windell *et al.,* 1978; Andrews, 1979; Storebakken & Austreng, 1987; Chakraborty *et al.,* 1995) or lipid digestibility but significantly reduced energy, carbohydrate and dry matter digestibility in fish fed the highest feeding rate (Windell *et al.,* 1978).

Strong correlations were found between digestibility of protein and digestibility of dry matter (Table 4). A large fraction of ingested dry matter is protein, so this would be expected. The high correlation between phosphorus digestibility and protein and dry matter digestibility could not be easily explained although it has also been observed in gilthead sea bream, *Sparus aurata* (Fernández *et al.,* 1998).

Henken *et al.* (1985) determined gross energy, dry matter and protein digestibility using three different methods in African catfish, *Clarias gariepinus* and nutrient digestibility negatively correlated with feeding level. ADC for energy in rainbow trout (Andrews, 1979) dry matter and protein in Nile tilapia, *Oreochromis niloticus* (Xie *et al.,* 1997) and fat in agastric common carp, *Cyprinus carpio* (Yamamoto *et al.,* 2001) negatively correlated with increasing feeding rate. Yamamoto *et al.* (2001) found that protein and starch digestibility slightly decreased with increasing feeding rate. In contrast, Cui *et al.,* (1994) found lower digestibility for protein at the lowest intake and higher digestibility for dry matter at highest intake in grass carp, *Ctenopharyngodon idella* and there was a tendency for digestibility to increase at higher intake that was in agreement with the present study. Increasing feeding rate of highly digestible diets would not affect nutrient digestibility or have small effect on them. However, a substantial decrease in digestibility would be expected in low quality diets. This is one reason why the major effects of feeding rate on digestibility results have been contradictory (Fernández *et al.,* 1998).

Apparent protein digestibility may be lower at lower feeding rates due to a relatively higher loss of endogenous faecal nitrogen (Azevedo *et al.,* 1998; Bureau *et al.,* 2002). Generally, apparent protein digestibility is 2-3% lower than true digestibility due to endogenous faecal nitrogen, so when low protein diet are fed the endogenous faecal nitrogen will constitute a larger part of the total faecal nitrogen (Jobling, 1994). Lower protein digestibility (3%) in fish fed lowest amount of feed in the present study is likely to be explained by this. Similarly, it is proposed that the lower phosphorus digestibility is attributed to relatively higher endogenous faecal phosphorus excretion.

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