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Effect and interaction of rainbow trout strain (*Oncorhynchus mykiss*) and diet type on growth and nutrient retention

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Abstract

Eight strains of rainbow trout were introgressed to develop a single strain (H-ARS) that was selected for faster growth when fed a fishmeal-free, plant-based diet (Selection Diet). For four generations, families from these crosses were fed the Selection Diet and selected for increased weight gain. Growth and nutrient retention were compared among H-ARS and two parental strains, the House Creek (HSC) and Fish Lake (FL) fed either a fish meal or Selection diet for 12 weeks. There was a significant effect of strain ($P < 0.01$), but not diet on weight gain, and a significant interaction of strain by diet ($P < 0.05$). The H-ARS trout gained more weight averaged across diet (991% of initial wt.) than the HC (924%) or FL trout (483%). The FL trout fed the fish meal diet gained more weight than FL trout fed the selection diet (510% vs 456%). Conversely, H-ARS trout fed the plant-based diet gained more weight than those fed the fish meal diet (1009% vs 974%). HSC trout had similar weight gain fed either diet (922% vs 926%). A significant effect of strain on protein retention ($P < 0.01$) was observed, along with a significant strain by diet interaction ($P < 0.02$). The results demonstrate that rainbow trout can be selectively improved to grow on a plant-based diet.

Keywords: rainbow trout, plant-based diet, selection, growth

Introduction

Aquaculture production is expanding significantly around the world. One of the major impediments to both current and developing aquaculture production is the availability of sustainable sources of feed (Naylor, Hardy, Bureau, Chlu, Elliott, Farrell, Forster, Gatlin, Goldburgh, Hua & Nichols 2009). Currently, fishmeal is the major protein source utilized in a number of aquaculture diets, especially for piscivorous and carnivorous species. Current use of fishmeal is nearing 70% of total production with predictions that global aquaculture demands will exceed availability within the next 10 years (Food & Agriculture Organization of the United Nations 2009). For decades, researchers have been evaluating alternative protein sources to replace fishmeal as the major protein component in aquaculture diets (Robinson & Meng 1994; Skonberg, Hardy, Barrows & Dong 1998; Torstensen, Espe, Sanden, Stubhaug, Waagbe, Hemre, Fontanillas, Nordgarden, Hevroy, Olsvik & Berntssen 2008). The use of formulated plant-based diets has been reported for many different species (Papatryphon 2001; Fontainhas-Fernandes, Gomes, Reis-Henriques & Coimbra 2009). However, there have been no reports of a piscivorous species of fish demonstrating better growth on diet formulated with the fishmeal protein completely replaced with plant protein.

To effectively replace as much fishmeal as possible with protein from plant sources, different methods have been employed to increase the protein availability of these products. These approaches include different processing methods used to increase protein levels, enhance positive material aspects and reduce anti-nutritional factor levels in plant-based fishmeal replacement diets (Gatlin, Barrows, Brown, Dabrowski, Gaylord, Hardy, Herman, Hu, Krogdahl, Nelson, Overturf, Rust, Sealey, Skonberg, Souza, Stone, Wilson & Wurtele 2007). Most reports showing growth comparisons between fish reared on standard fish meal diets compared with diets where fishmeal is replaced with alternative protein ingredients, typically plant, report a significant reduction in growth in the fish reared on the diets containing alternative protein sources (Kaushik, Cravedi, Sumpter, Fauconneau & Laroche 1995; Cheng & Hardy 2003; De Francesco, Parisi, Medale, Lupi, Kaushik & Poli 2004). Genetic enhancement of existing piscivorous and carnivorous stocks of fish is another approach for improving growth and utilization of plant-based feeds. Genetic variation has been found, and in some cases, used to improve traits such as disease resistance, growth rate, feed efficiency, offspring size, quality traits, morphology and others in agricultural animals (Mrode & Kennedy 1993; Heringstad, Klemetsdal & Ruane 2000; Baeza, Dessay, Wacrenier, Marche & Listrat 2003). Meanwhile, in aquaculture, selective breeding has been shown to improve salinity tolerance, growth and disease resistance (Dunham, Brady & Vinitnantharat 1994; Rezk, Smitherman, Williams, Nichols, Kucuktas & Dunham 2003; Kamal & Mair 2005).

Research has been conducted to determine the relative genetic potential for improving growth of certain fish species fed specific plant-based feeds. Palti (Palti, Silverstein, Wieman, Phillips, Barrows & Parson 2006) found no change in the rankings of 20 full-sib families of rainbow trout for growth when the fish were fed a fishmeal or a plant protein-based diet. However, the plant-based diet used in Palti's study contained 10% krill. However, a later study using whitefish (*Coregonus lavaretus*) found substantial genetic variation for growth traits between families fed either a fishmeal diet or a diet with 50% of the protein replaced with soybean meal (Quinton, Kause, Koskela & Ritola 2007). Furthermore, a more recent study using diets where fishmeal was completely replaced found significant genetic variation in growth for salmonids (*Oncorhynchus mykiss*) fed plant-based feeds (Pierce, Palti, Silverstein, Barrows, Hallerman & Parsons 2008). Similar results comparing marine ingredient-based diets against diets where the fishmeal and fish oil is completely replaced by plant products were found in sea bream (Le Boucher, Vandeputte, Dupont-Nivet, Quillet, Mazurais, Robin, Vergnet, Medale, Kaushik & Chatain 2011).

Although these and other studies were done to determine genetic variance and the potential heritability for growth and utilization of a plant-based diet, no studies have been reported using fish that had been selected for growth on a fishmeal-free, plant-based feed for several generations. From variability previously detected in studies in rainbow trout, and the need for improved strains, a selection programme was initiated in 2000 to generate a strain of rainbow trout with improved growth characteristics when reared on a fishmeal-free, plant protein-based diet. Reported here is the growth performance of this selected strain of rainbow trout after four generations of selection in comparison to two of the parental stocks, a fast growing domesticated strain and a slower growing conservation strain.

Materials and methods

Fish stocks

Fish strains used in this study consisted of a domesticated strain selected for growth for several generations (Housecreek) (Overturf, Casten, LaPatra, Rexroad & Hardy 2003), a strain reared by US Fish and Wildlife Service (Ennis, MT) and used for stocking in streams and lakes (FishLake) and a strain generated by introgression and selection (Hagerman-ARS). The Hagerman-ARS (H-ARS) strain was introgressed with the following fish strains; Oregon and Housecreek (HSC) from the College of Southern Idaho Hatchery in Twin Falls, Idaho; R9 and Kamloops from the Idaho State Fish Game Hatchery in Hayspur, Idaho; Fish Lake (FL), Shasta, and Arlee from the US Fish and Wildlife Hatchery in Ennis, Montana; and the Donaldson strain from the University of Washington, Seattle, Washington. The H-ARS stock has been selected for growth on a plant-based diet (Table 1) containing fish oil, but without fishmeal. Selection pressure on the H-ARS stock has been maintained for four generations by retaining the top 15% (as assessed by weight) of the fish from the 40 best performing families for each year class(as assessed by family average for specific growth rate and feed conversion ratio at 6 months post feeding) as broodstock. Fish rearing was carried out at the University of Idaho's Hagerman Fish Culture Experiment Station. Experiments were carried out in 140 L tanks supplied with constant 15°C temperature spring water at a flow rate of approximately 11.5 L min^{-1}. Photoperiod was maintained at 14 h light:10 h dark. The composition of the two diet formulations, the fishmeal control and the plant protein selection diet, are shown in Table 1. Fish were handled and treated according to the guidelines of the University of Idaho's Institutional Animal Care and Use Committee.

Table 1 Ingredient and nutrient composition of standard control fishmeal diet and plant meal selection diet

	g kg^{-1}	
Ingredient	**Fish meal**	**Plant meal**
Soy protein concentrate[*]	—	256.3
Corn protein concentrate[†]	61.6	175.4
Wheat gluten[‡]	—	4.1
Soybean meal[§]	158.4	19.6
Fish meal[¶]	336.0	—
Wheat starch[**]	262.3	891.0
Blood meal[††]	58.5	—
Poultry meal[‡‡]	46.5	—
Menahaden oil[§§]	120.6	157.0
Vitamin premix[***]	10.0	10.0
Methionine	2.9	3.8
Taurine	5.0	5.0
Dicalcium phosphate	—	33.3
Trace min. premix[¶¶]	1.0	1.0
Choline CL	1.1	6.0
Stay-C	0.3	2.0
Potassium chloride	—	5.6
Magnesium oxide	—	0.6
Sodium chloride	—	3.8
	Calculated composition, as is basis	
Crude protein, g kg^{-1}	444.0	444.4
Crude fat, g kg^{-1}	160.8	160.7
Phosphorus, g kg^{-1}	11.0	11.3

[*] Solae, Pro-Fine VF, 693 g kg^{-1} crude protein.

[†] Cargill, Empyreal 75, 761.0 g kg^{-1} protein.

[‡] Manildra Milling, 750 g kg^{-1} protein.

[§] ADM Inc., 480 g kg^{-1} protein.

[¶] Omega Proteins, Menhanden Special Select, 628 g kg^{-1} protein.

[**] Manildra Milling, 4 g kg^{-1} protein.

[††] IDF Inc., 832 g kg^{-1} protein.

[‡‡] American Dehydrated Foods, 734 g kg^{-1} protein.

[§§] Omega Proteins Inc.

[¶¶] Contributed in mg kg^{-1} of diet; zinc 40; manganese 13; iodine 5; copper 9.

[***] Contributed, per kg diet; vitamin A 9650 IU; vitamin D 6600 IU; vitamin E 132 IU; vitamin K3 1.1 gm: thiamin mononitrate 9.1 mg; riboflavin 9.6 mg; pyridoxine hydrochloride 13.7 mg; pantothenate DL-calcium 46.5; cyancobalamin 0.03 mg; nicotinic acid 21.8 mg; biotin 0.34 mg; folic acid 2.5; inostitol 600.

Experimental setup and sampling

Three strains of rainbow trout, Housecreek (HSC), FL and H-ARS, were stocked into 18 140 L tanks (six tanks per strain) at 35 fish per tank. The average fish weight of the fish was 30 ± 1.6 g. The fish strains were stocked randomly among tanks and three tanks of each strain of fish were fed either the fishmeal control diet (FM) or the plant-based selection diet (PB) (Table 1). The fish were fed to apparent satiation twice daily, 6 days a week, for 12 weeks. The fish from each tank were bulk-weighed and counted every 4 weeks, and the amount of feed fed to each tank was recorded daily throughout the experiment. Whole body samples were taken (five fish per tank) every 4 weeks throughout the experiment.

Diet preparation

Both the fishmeal control diet and the selection diet were produced with commercial manufacturing methods using a twin-screw cooking extruder (DNDL-44, Buhler AG, Uzwil, Switzerland) at the Bozeman Fish Technology Center, Bozeman, MT. Diet mash was exposed to an average of 114°C for 18-s in five barrel sections, and the last section was water cooled to an average temperature of 83°C. Pressure at the die head was approximately 450 psi. The pellets were then dried in a pulse bed drier (Buhler AG) for 25 min at 102°C and cooled at ambient air temperatures to reach final moisture levels of < 10%. Fish oil was top-dressed using vacuum coating (A.J Flauer Mixing, Ontario Canada) after the pellets were cooled. Diets were stored in plastic lined paper bags at room temperature until used. All diets were fed within 4 months of manufacture.

Proximate analysis

Whole fish were pooled by tank and ground for homogeneity prior to analyses. Whole fish samples, individual fillet and diet samples were analysed in duplicate assays using standard AOAC (1995) methods for proximate composition. Dry matter and ash analysis was performed on a LECO thermogravimetric analyser (TGA701, LECO Corporation, St. Joseph, MI, USA). Protein (N × 6.25) was determined using the Dumas method (AOAC 1995) on a LECO nitrogen determinator (TruSpec N, LECO Corporation, St. Joseph, MI, USA) and was measured using a Foss Tecator Soxtec HT Solvent Extractor, Model Soxtec HT6 (Höganäs, Höganäs, Sweden). Total energy was determined using adiabatic bomb calorimetry (Parr 6300, Parr Instrument Company, Moline, IL, USA). Protein retention and energy retention efficiencies were calculated as follows:

$$\begin{aligned}&\text{Protein retention efficiency (PRE)}\\&= (\text{protein per gram of final fish weight}\\&-\ \text{protein per gram of initial weight})\\&\quad \text{protein gain} \times 100/\text{protein fed}\end{aligned}$$

$$\begin{aligned}&\text{Energy retention efficiency (ERE)}\\&= (\text{calculated energy of final fish tank weight}\\&- \text{energy of initial fish tank weight})\\&\times 100/\text{energy fed. Muscle ratios were}\\&\text{calculated by (fillet weight/body weight)}\\&\times 100.\end{aligned}$$

$$\begin{aligned}\text{Muscle Ratio} &= \text{Muscle Ratio (MR)}\\&= \text{fillet mass with ribs (g)}\\&\quad \times 100/\text{fish mass (g)}\end{aligned}$$

Statistical analysis

Microsoft Excel was used to graphically represent the data. Fish performance, nutrient retention and carcass composition data were analysed with the general linear models procedure using a factorial treatment design and the Statistical Analysis System (SAS 9.2; SAS Institute 2008, Cary, NC, USA). Tank mean values were considered units of observation for statistical tests, and mean values were considered significantly different when $P < 0.05$. Any value expressed as a percentage was arcsine transformed prior to analysis (Sokal & Rohlf 1981).

Results

Strain and dietary effects for growth and feed conversion

A significant effect on growth was seen for strain, but not diet (Fig. 1). Both the H-ARS and HSC strains of fish exhibited higher performance than the FL strain when fed the fishmeal control diet as evidenced by significantly higher final weights, weight gain, specific growth rate (SGR) and per cent weight gain. However, there were no significant interactions found in growth between the H-ARS and HSC strain fed the fishmeal control diet. On the plant-based selection diet, the H-ARS strain significantly outperformed both the HSC and FL strains in terms of weight gain, SGR and per cent weight gain, whereas the HSC strain showed significant improvement for all measured growth parameters over the FL strain when fed the plant-based selection diet. Comparison between diets for each strain showed that the FL strain grew significantly better when fed fishmeal control diet than when fed the plant-based selection diet. The HSC strain showed no significant differences in growth between the fishmeal and the plant-based diet. The H-ARS strain showed significant improvements in growth on the plant-based selection diet over the fishmeal feed (Table 2).

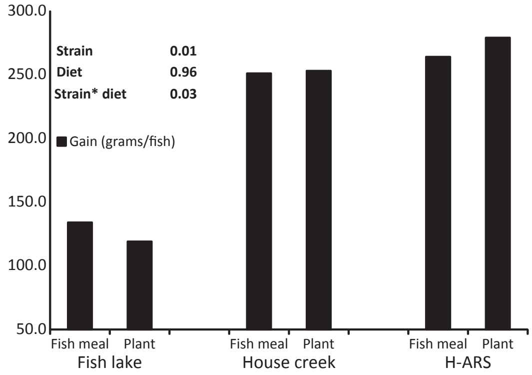

Figure 1 Comparison of weight gain for the Fish Lake, Housecreek, and H-ARS strains of fish on either a fishmeal or plant-based diet with significant interactions shown in legend.

There was a significant strain interaction on feed intake with both the H-ARS and HSC strains having a significantly higher feed intake than the FL strain on either of the diets. For FCR, there was a significant strain by diet interaction where FL was found to have a higher FCR on the fishmeal diet compared with the HSC and H-ARS strains, but showed no difference between the diets. The HSC strain showed significant differences for FCR between the diets with lower levels found on the fishmeal control diet. The H-ARS strain had no significant difference in FCR between the two diets (Table 2).

Dietary and strain effect on body composition and nutrient retention

No significant interactions were found within or between the strains and diets for protein, fat and

Table 2 The effect of diet and strain on growth and feed parameters of selected versus non-selected rainbow trout reared on either a fish meal or plant meal-based diet

Strain	Diet	Final weight, g fish^{-1}	Gain		Gain, % initial	Feed Intake	
			g fish^{-1}	SGR		% body wt.	FCR
Fish Lake	Fish meal	167	134.0	2.26	510	1.67	0.90
	Plant-based	152	119.0	2.11	456	1.61	0.91
House Creek	Fish meal	282	251.0	3.09	922	1.80	0.81
	Plant-based	283	253.0	3.09	926	2.08	0.93
H-ARS	Fish meal	294	264.0	3.16	974	1.95	0.86
	Plant-based	309	279.0	3.20	1009	2.03	0.89
	Probability of > F value						
Model		0.01	0.01	0.01	0.01	0.01	0.13
	Strain	0.01	0.01	0.01	0.01	0.01	0.48
	Diet	0.86	0.94	0.19	0.72	0.07	0.04
	Strain × diet	0.03	0.03	0.02	0.05	0.07	0.20
	CV	3.44	3.95	1.94	3.50	5.89	5.92
	R-square	0.98	0.99	0.99	0.99	0.79	0.47

SGR, specific growth rate; FCR, feed conversion ratio.

Table 3 The effect of diet and strain on body composition and nutrient retention of selected and non-selected rainbow trout fed either a standard fishmeal control or plant-based selection diet

Strain	Diet	Moisture	Body composition				PRE	ERE
			Protein	Fat	Ash	cal g^{-1}		
Fish lake	Fish meal	68.2	16.8	13.1	1.90	6741	20.2	40.9
	Plant-based	67.4	17.1	12.8	2.10	6744	17.1	40.7
House creek	Fish meal	68.9	16.4	12.7	1.90	6727	41.2	40.0
	Plant-based	67.5	16.6	13.6	2.10	6848	42.7	41.7
H-ARS	Fish meal	68.6	16.9	12.5	2.00	6704	45.6	40.2
	Plant-based	67.7	16.5	13.4	2.00	6828	47.3	41.3
	Probability of > F value							
Model		0.13	0.38	0.70	0.49	0.20	0.01	0.47
	Strain	0.83	0.83	0.41	0.93	0.61	0.01	0.99
	Diet	0.01	0.14	0.81	0.07	0.04	0.94	0.12
	Strain × diet	0.51	0.26	0.62	0.74	0.33	0.02	0.38
	CV	0.96	5.37	3.44	8.37	1.14	4.03	2.75
	R-square	0.47	0.33	0.20	0.28	0.42	0.99	0.29

Cal g^{-1}, calories per gram; PRE, protein retention efficiency; ERE, energy retention efficiency.

ash content. However, there was a significant interaction for moisture between the diets. No significant interactions were found for energy retention. However, there were significant strain and diet-by-strain interactions found for protein retention efficiency (Table 3). The H-ARS and HFS showed significantly higher protein retention efficiencies than the FL strain for both diets. Furthermore, the H-ARS strain showed higher protein retention efficiencies than the HSC strain for both diets (Fig. 2). No significant interactions were found in muscle ratios between any of the strains of fish for either diet.

Discussion

Production of commercial aquaculture diets utilizing protein from sustainable sources will constrain rising feed costs and maintain more stable feed prices in the future. With this in mind, there has been extensive research effort invested in improving the formulation of diets to enhance growth

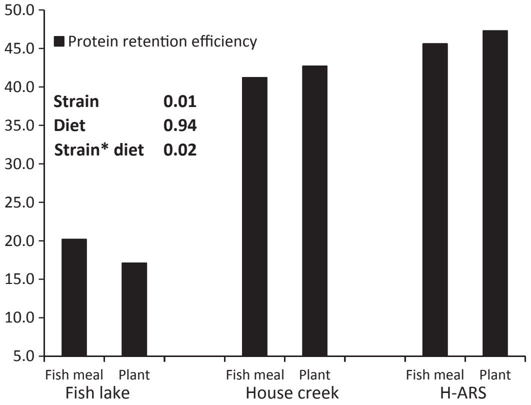

Figure 2 Comparison in protein retention efficiency for the Fish Lake, Housecreek, and H-ARS strains of fish on either a fishmeal or plant-based diet with significant interactions shown in legend.

and utilization and to test and develop sustainable economical feeds (Gatlin *et al.* 2007). Further research has been done to evaluate and determine the potential to improve the performance of fish using selective breeding, so that they grow more efficiently and utilize feeds containing sustainable protein sources (Quinton *et al.* 2007; Pierce *et al.* 2008). Although many different feeds incorporating almost every conceivable plant product have been tested, with many providing reasonable growth and FCRs, researchers have not yet been able to equal the growth found with fishmeal-based diets for piscivorous and carnivorous species. There are multiple reasons why a feed containing plant protein instead of fishmeal would reduce growth, including the presence of saponins, protease inhibitors, lectins and other anti-nutritional factors, improper amino acid balance, lack of steroids present in fish meal, reduced availability of certain minerals and vitamins and reduced palatability (Francis, Makkar & Becker 2001; Gatlin *et al.* 2007; Glencross, Booth & Allan 2007). However, the record on selecting carnivorous fish to grow more efficiently on these plant-based diets is mixed. A number of studies evaluating genetic variation in aquaculture species have determined both positive and negative potential for certain species on different formulated fishmeal diets (Palti *et al.* 2006; Pierce *et al.* 2008; Le Boucher *et al.* 2011; Quinton *et al.* 2007).

A major issue of improving growth on a fishmeal replacement diet is lack of knowledge on what physiological or metabolic changes result in reaction to specific plant nutrient components. There are several physiological changes that could be taking place independently or interactively depending on the dietary makeup of the feed. Selection might involve improving tolerance to anti-nutritional factors, increasing overall feed intake, palatability senses, amino acid sensing and regulation or metabolic regulation involving vitamins and minerals, or a possible combination of these different actions. Furthermore, compounding the complexity is how different diet formulations or nutrient components might affect each of these components and how variations in fish strains play a role. Alternatively, the deleterious overabundance or lack of one or more specific nutrients might obscure positive genetic variation for the growth and utilization of other dietary components. Previous studies have all differed in their findings and this could most likely be attributed to differences in the diets, dietary components and the stocks of fish used.

In the present work, families from several rainbow trout strains were first tested for variation in growth when fed a plant-based diet versus a standard fish meal diet. After it was established that sufficient variation was present, a selection programme was instigated involving the introgression of eight fish stocks reared on an economically feasible plant-based feed. The fish used in the current study had been under selection for growth for four generations, and over this period, their average weight when grown on the plant-based selection diet increased from an average of 178 to 256 g at 5 months from first feeding with an average realized heritability of 0.42. From other unreported studies, we have observed that these fish under selection perform better on high carbohydrate diets (35%), have increased tolerance for low palatability feeds and improved intestinal health when fed plant-based feeds when compared with non-selected fish (unreported data). In this study, we compared the growth of these 4th generation selected stocks to two initial strains of fish, a fast growing domesticated strain and a strain used in conservation stocking, that were part of the initial introgressed stocks used in development of the H-ARS strain of trout. Previous studies have reported that even with the best formulated plant-based feeds, trout and salmon weight gain was typically at least 10% reduced compared with practical fishmeal based feeds (Carter & Hauler 2000; Cheng & Hardy 2003). In the present study, selected fish showed no significant difference in weight gain or

SGR with the fast growing domesticated strain on the control fishmeal diet, but had significantly better SGR and weight gains and showed improved protein retention efficiency on the plant-based diet used in selection. This is the first report whereby a stock of fish has been shown to have grown faster when fed an all-plant-based feed compared with a fishmeal based feed.

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