Feed efficiency of rainbow trout can be improved through selection: Different genetic potential on alternative diets[1]

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ABSTRACT: To assess the genetic potential for selection of increased feed efficiency in rainbow trout (*Oncorhynchus mykiss*), we estimated the heritabilities and correlations for BW, daily weight gain (DG), and daily feed intake (DFI). Body weight was recorded 5 times, and DG and DFI 3 times during a feeding trial lasting 22 mo. To test the hypothesis that phenotypic and genetic parameters were influenced by a nutritional environment, fish were fed either a modern normal protein diet (NP, 40 to 45% protein and 30 to 33% lipid) or an alternative high protein diet (HP, 50 to 56% protein, 20 to 24% lipid) in a split-family design. Results showed that there were no large differences in heritabilities between the diets. Average heritability for DFI over both diets and different fish ages was low (average h^2 = 0.10), indicating that modest genetic changes in response to selection can be obtained. Average heritabilities for BW and DG over both diets and different fish ages were 0.28 and 0.33, respectively. The NP diet enabled fish to express a wide range of BW, as shown by the increased coefficients of phenotypic variation for BW. Fish fed the HP diet showed increased phenotypic variation for DFI in >750-g fish. On the NP diet, genetic correlations of DFI with DG and BW were very strong for 750- to 2,000-g fish. In contrast, on the HP diet, the respective correlations were moderate to low, revealing more genetic potential to change growth and feed intake simultaneously in opposite directions. An analysis of the predicted selection responses showed that selection solely for high DG improved feed efficiency as a correlated genetic response. Simultaneous selection for high DG and reduced DFI, in turn, may increase genetic gain in feed efficiency by a factor of 1.2 compared with selection solely for DG. However, variation for growth and feed intake and the relationships between these traits were different in different nutritional environments, leading to divergent genetic responses on the alternative diets.

Key words: feed efficiency, feed intake, genotype-by-environment interaction, heritability, quantitative genetics, rainbow trout

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INTRODUCTION

Studies on the quantitative genetics of feed efficiency in fish are lacking. Moreover, it is possible that current commercial fish feeds impose unfavorable genetic constraints that hamper selection efforts to improve feed efficiency. Here, we estimated heritabilities and genetic correlations for daily feed intake (**DFI**), daily weight gain (**DG**), and BW in rainbow trout fed 2 diets; a normal protein (**NP**) diet representing a modern feed, and an experimental high protein (**HP**) diet.

It was hypothesized that the selection potential for feed efficiency should be greater on an HP diet. First, we hypothesized that phenotypic and genetic variation in growth should be greater on an HP diet, allowing greater selection responses than on an NP diet. This is based on the idea that on an NP diet, protein growth is restricted due to the low dietary protein level (Kim and Kaushik, 1992), and high lipid level of NP diet

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facilitates high lipid deposition in the body of all individuals. This is assumed to lead to similar wet weight growth among individuals, regardless of their growth composition, thereby reducing variation.

In contrast, on an HP diet, the variation in BW is increased because of the variation in the capacity of fish to utilize dietary protein for growth (protein efficiency; Houlihan et al., 1995). Due to the high protein content of an HP diet, the capacity of inefficient fish to deposit digested protein as protein growth is greatly exceeded (Kim and Kaushik, 1992), and the low lipid content restricts their lipid growth. This results in poor overall growth of the inefficient fish, and hence, leads to increased variation on HP diet.

Second, we tested whether growth and feed intake were strongly correlated, as has been shown in farm animals (e.g., Clutter and Brascamp, 1998). Moreover, we tested whether this tight correlation could be uncoupled on the HP diet, enhancing the selection potential. Third, we assessed the usefulness of different selection strategies to improve feed efficiency.

MATERIALS AND METHODS

Population Structure

The rainbow trout (*Oncorhynchus mykiss* Walbaum) used in this study belonged to the Finnish national breeding program. All fish were housed at the Tervo Fisheries Research and Aquaculture station (a freshwater station) of the Finnish Game and Fisheries Research Institute for the duration of the experiment (June 2001 to November 2004). The breeding scheme was reported previously by Kause et al. (2005).

To estimate genetic parameters, the 2001 generation was exposed to the 2 different diet treatments in a split-family design. The pedigree for every fish was known as far back as 4 generations. A total of 210 full/half-sib families were produced from 89 sires and 109 dams of 3 yr of age in a factorial mating design. Matings were completed during 3 d. Full-sib batches of eye-staged eggs were transferred to indoor 150-L family tanks in June 2001.

In February 2002, after 8 mo of growing in the family tanks, 2,931 fingerlings were removed from the family tanks, and individually tagged with PIT-transponders (Trovan Ltd., Köln, Germany) to enable individual identification. For 45 of the 210 full-sib families, an average of 39.6 individuals per family (range: 37 to 40) were randomly tagged. The large initial family size was used because these families were later sampled not only for BW and feed intake but also for destructive composition traits necessary for a parallel study (our unpublished observations). For the remaining 165 full-sib families, nondestructive sampling was planned, so an average of 7 fish per family (range: 4 to 7) were randomly tagged.

Fish Management

During tagging in February, each family was randomly split into 2 groups to be reared with different experimental diets. In May 2002 (at wk 20), the 2 diet treatments were initiated. Before the initiation of the diet treatments, all fish were fed with commercial rainbow trout dry food (Nutra Starter and Nutra Parr, Rehuraisio Inc., Raisio, Finland). The experimental diets were a modern diet with low protein (40 to 45% of DM) and high lipid content (30 to 33% of DM; NP diet), and an alternative diet with high protein (50 to 56% of DM) and low lipid content (15 to 24% of DM; HP diet; Table 1). The diets consisted of fish meal, fish oil, wheat meal, and wheat starch, and were supplemented for minerals and vitamins according to National Research Council (1993) recommendations.

The fish assigned to the 2 diets did not differ in weight at tagging (mean ± SD; NP = 62.4 ± 19.9 g, n = 1,355; and HP = 62.3 ± 19.4 g, n = 1,335). Each diet group was equally divided into 4 replicate fiberglass tanks and housed indoors. The fish were kept in 3-m^3 tanks until wk 24, and transferred to 20-m^3 tanks thereafter. The families were equally distributed among the tanks. Fish density in the tanks was under 20 kg/m^3.

Feed was provided 4 h a day by computer-controlled pneumatic feeders (Arvo-Tec Inc., Huntokoski, Finland). To ensure overfeeding and to prevent restriction of the growth potential of the fish, feed consumption was controlled daily by visual observation. Feeding was regarded as overfeeding when uneaten feed remained on the bottom of the tanks after 4 h of feeding. The amount of excess feed was 10 to 20% over the recommendations of the feed company. Water temperature during the experiment was ambient, with seasonal fluctuations.

Recording Traits

The approach we adopted here follows the logic that genetic components of feed efficiency (DG:DFI) can be sufficiently described by the analysis of its constituent traits, DG and DFI (Gunsett, 1984; Kennedy et al., 1993; Cammack et al., 2005). The disadvantage of analyzing feed efficiency per se is that a trait defined as a ratio is often ill behaved statistically, and it is difficult to control which of its component traits is changing when selection is applied on the ratio. Moreover, genetic parameters of feed efficiency are determined by its component traits, and feed efficiency can be improved by selecting for the component traits with appropriate economic weights (Gunsett, 1984; Kennedy et al., 1993).

Body weight was recorded 5 times: in May 2002 (time 1), October 2002 (time 2), May 2003 (time 3), September 2003 (time 4), and November 2003 (time 5; traits: BW_1 to BW_5). Daily feed intake was recorded 3 times: at times 1, 2, and 4 (traits: $DFI_{1,2,4}$). The average family sizes at different times are given in Table 2.

Recording times 1, 2, and 4 consisted of a 3-wk x-ray session with 3 repeated measurements of BW and DFI. The x-radiography was used to record individual feed consumption, using a portable x-ray unit (Todd Research 80/20, Essex, UK), as described by Talbot and

Table 1. Proximate composition[1] of normal protein (NP) and high protein diets (HP), including glass bead-labeled x-ray diets fed at measurement times 1 (bead size, 3 mm), 2 (bead size, 6 mm), and 4 (bead size, 7 mm)

Diet, pellet size	Moisture (%)	Ash (%)	CL (%)	CF (%)	CP (%)	NFE (%)	P (g/kg)	Energy (kJ/g)
NP, 3 mm	2.1	7.4	30.5	0.73	44.9	15.1	12.1	23.6
NP, 6 mm	1.5	7.7	30.3	0.72	44.6	15.9	12.7	26.0
NP, 7 mm	4.0	6.7	33.4	1.00	39.5	15.4	9.60	25.9
HP, 3 mm	2.3	9.6	20.7	0.44	56.4	11.1	15.5	25.6
HP, 6 mm	1.7	9.5	20.6	0.48	56.3	11.9	15.4	24.0
HP, 7 mm	7.2	8.3	23.8	1.30	49.4	10.0	11.8	23.3
NP, 3 mm (labeled)	6.9	7.5	29.4	0.74	41.1	15.1	11.3	24.3
NP, 6 mm (labeled)	5.6	7.4	31.4	0.72	40.1	15.5	11.2	24.9
NP, 7 mm (labeled)	3.8	6.3	34.3	1.00	40.5	14.1	10.4	25.6
HP, 3 mm (labeled)	7.6	10.4	15.4	0.62	54.2	12.4	15.2	21.1
HP, 6 mm (labeled)	9.4	10.6	14.1	0.55	54.1	11.8	15.1	20.7
HP, 7 mm (labeled)	3.9	9.1	20.6	0.90	55.8	9.70	13.8	22.4

[1]Composition is on a DM basis; CL = crude lipid; CF = crude fiber; NFE = nitrogen-free extracts.

Higgins (1983). During each 3-wk session, each of the 8 tanks was measured once weekly (1 NP and 1 HP tank per day) in the same order each week. To avoid the potential effects of systematic feeding rhythms, the recording order of NP and HP tanks was reversed on successive days.

To initiate a recording session, all fish (x-ray and non-x-ray) were weighed during the first week of each session, and DFI was measured from randomly selected individuals from each family. In the second and the third weeks, the procedure was repeated but only the fish x-rayed in the first week were reweighed and x-rayed again. A 1-wk difference between DFI recordings was considered appropriate because fish appetite is reduced very little, even during the day following x-raying (McCarthy et al., 1993).

The x-rays were performed in the same way for all tanks during all sessions. Before x-ray, all fish from a given tank were fed as usual but the diet was labeled with radio-opaque ballotini glass beads (Jencons Scientific Ltd., Leighton Buzzard, UK; Table 1). The labeled pellets used at times 1, 2, and 4 consisted of 1, 0.5, and 0.3% beads, respectively, with a diameter of 400 to 600 μm. To avoid increased time and labor needed for counting the beads of large fish, bead density was reduced with increasing fish age. This is because larger fish consume more, and thus the reduced bead density prevents the absolute bead number within a fish from being elevated and unnecessarily large.

Table 2. Population structure and average family size of the 210 full/half-sib families used[1]

Item	165 families	45 families
No. of sires, dams	81, 99	34, 40
Family size, time 1[2]	6.6	30.9
Family size, time 2	5.4	26.6
Family size, time 3	5.2	15.6
Family size, time 4	4.4	13.4
Family size, time 5	4.1	12.9

[1]High family size in 45 families was needed due to destructive sampling.
[2]Five sampling times distributed between May 2002 and November 2003.

A minimum of 2 h after the feeders had stopped providing feed, the fish to be recorded were serially placed into anesthetic solution (buffered MS-222, Argent Laboratories, Redmond, WA), weighed, and x-rayed. Thereafter, the beads were counted from the films, and the weight of feed within a stomach was estimated using a calibration regression equation. The predictive calibration equation was constructed for each session and each diet separately by x-raying different but known amounts of feed (n = minimum of 8 feed samples), and then by regressing the number of counted beads from the films against the known feed weight (R^2 = 0.90 to 0.99). Evacuation of the feed before x-ray was avoided by adjusting the duration of the feeding and the length of the recording period, using information from a separate experiment (data not shown).

At times 3 and 5, each fish was anesthetized and recorded for BW once. The fish were recorded for sex and maturity at time 3 by a visual inspection of secondary sexual characters, and at time 5 by the examination of gonads from slaughtered fish. Six sex × maturity classes were identified: males that were mature at 2, 3, and later years; females that were mature at 3 and later years; and fish with unknown sex and maturity age.

Traits Analyzed

Feed intake was measured daily. For this reason, we also calculated growth from BW records as DG. Daily gains at times 1, 2, and 4 for each individual were calculated following the methods of Iwama and Tautz (1981) and Cho (1992), and using information on the daily water temperature and on the 2 to 3 repeated BW records obtained for each x-rayed individual during each x-ray session (traits: $DG_{1,2,4}$). First, a growth rate

(the regression coefficient b_i) for the ith fish over a 3-wk period was calculated from a regression:

$$BW_{ij}^{1/3} = a + b_i\, CTEMP_j + e_{ij}, \quad [1]$$

where $BW_{ij}^{1/3}$ is the cubic root of the BW record measured for individual i during day j, a is an intercept of the regression, $CTEMP_j$ is a cumulative temperature sum at day j, and e_{ij} is the residual. Then, DG for each individual was obtained using the following equation:

$$DG_{ij} = (a + b_i\, CTEMP_{j+1})^3 - (a + b_i\, CTEMP_j)^3, \quad [2]$$

where the terms in parentheses are the predicted cubic root BW during 2 successive days (j and j+1) obtained using Eq. 1. In other words, day j is the day when a fish was measured for BW (and x-rayed) and day j+1 is the consecutive day. Using this method, DG (in units of g/d) can be calculated for each individual with 2 or more BW records.

Next, for each individual at each 3-wk x-ray session, the repeated observations for DFI, DG, and BW were each compressed into a single (more accurate) mean. This approach was justified because salmonids have extremely high day-to-day variability in feed intake compared with other domesticated animals. For instance, an individual fish does not feed every day or may feed very little on some days (McCarthy et al., 1992; Jobling and Koskela, 1996). This is indicated by the low repeatability of DFI (r = 0.09 to 0.32; our unpublished observations). Thus, single-point estimates of DFI are potentially inaccurate, and averaging several repeated observations increases the measurement accuracy considerably (Falconer and Mackay, 1996).

Because some of the x-rayed fish lacked 1 of the 3 observations within a session and because of the differences among the average daily trait means, the raw means for each individual would have been unsuitable for the subsequent calculations. Therefore, weighted least squares means for each individual were obtained by accounting for the test tank-wise weekly performance. This was performed for each tank separately by fitting an ANOVA to the longitudinal feed intake data with a model including individual fish (all fish within a given test tank) and test week (wk 1, 2, and 3) as factors, and calculating least squares means for each individual (LSMEANS option, SAS Inst., Inc., Cary, NC). Because test tanks were treated separately, the test tank differences remained in the data and needed to be fitted in the subsequent statistical analyses. These least squares means at times 1, 2, and 4 were used as observations in the subsequent statistical and genetic analyses. The measures of BW_3 and BW_5 included only 1 record, so least squares means were not required.

Statistical Tests for Diet Differences in Trait Means

To examine the differences between the diets in the trait means, parametric ANOVA were performed for each trait separately (Proc Mixed; SAS Inst., Inc.). The fixed effects included in the model were diet, sex × maturity class, and the interaction of diet with sex × maturity class. The random factors included were test tank nested within diet, family (this consists of both common environmental effects and genetic effects of full-sib families), interaction of test tank with sex × maturity class, interaction of family with diet, and interaction of family with sex × maturity class.

The method of Kenward and Roger (1997) was used to calculate the correct degrees of freedom and *F*-tests for the fixed effects. All DFI values were transformed using square roots to obtain normally distributed residuals. When calculating statistical tests and least squares means for fish with equal size, BW was included as a covariate in the models of DFI and DG. We refer to these traits corrected for BW as $DFI\%_{1,2,4}$ and $DG\%_{1,2,4}$. Performing a repeated analysis of BW, DG, and DFI to compare diet differences across time was not possible because the extensive data size and complex mixed model led to memory capacity problems when using PROC MIXED.

Genetic Analyses

(Co)variance components were estimated using the DMU AI software that was developed for analyzing multivariate mixed models using the restricted maximum likelihood method (Jensen and Madsen, 2000).

A trait measured on the 2 diets was regarded as 2 different traits. The model for the diet-specific traits was:

$$y_{ijkl} = anim_i + famtank_j + SEXMAT_k + TESTTANK_l + \varepsilon_{ijkl}, \quad [3]$$

where $anim_i$ is a random additive genetic effect of an animal (i = 1...number of observations), $famtank_j$ is a random family tank effect (j = 1 to 210 tanks), $SEXMAT_k$ is a fixed sex and maturity effect (k = 1 to 6), $TESTTANK_l$ is a fixed test tank effect (l = 1 to 4 tanks), ε_{ijkl} is the residual, and y_{ijkl} is an observation from individual i. When analyzing multitrait models with 2 traits measured on different diets, the residual covariance was set to zero.

To obtain genetic parameters for feed intake percentage (DFI adjusted for BW) and daily gain percentage (DG adjusted for BW), BW was included as a covariate into the models of raw DFI and DG. Body weight-adjusted DFI and DG are of interest in assessing the degree to which family differences (heritabilities) and ranking of families across diets (between-diet correlations) are a result of BW differences. They are not, however, needed for the analysis of feed efficiency genetics because the analysis of the components, raw DG and DFI, will suffice.

Heritabilities and genetic correlations between diets were obtained from bivariate models including the same character recorded on both diets. To obtain trait

correlations within diets, a multitrait model with BW, DG, and DFI was run separately for each diet and each sampling time.

Using these models, additive genetic (σ^2_A), common environment due to shared environment of full sibs during incubation and family tank rearing ($\sigma^2_{\text{fam tank}}$), residual ($\sigma^2_R$), and phenotypic variances ($\sigma^2_P = \sigma^2_A + \sigma^2_R + \sigma^2_{\text{fam tank}}$), as well as phenotypic (r_P) and genetic correlations between traits (r_A) were obtained. Heritability was calculated as $h^2 = \sigma^2_A/\sigma^2_P$ and common environment ratio as $c^2 = \sigma^2_{\text{fam tank}}/\sigma^2_P$. If the common environment ratio was lower than 0.01, the family tank effect was removed from the model of that trait. To scale the phenotypic variance of traits with different means ($\bar{x}$), coefficient of phenotypic variation was calculated as $CV_P = \sqrt{\sigma^2_P}/\bar{x}$. Because heritability is a ratio, low heritability can result either from low genetic variation or from high residual variation, or both. Thus, we calculated coefficients of additive genetic variation $CV_A = \sqrt{\sigma^2_A}/\bar{x}$ and of residual variation $CV_R = \sqrt{\sigma^2_R}/\bar{x}$ (Houle, 1992).

RESULTS

Diet Effects

Neither BW nor daily gain differed between diets ($P > 0.08$; Table 3). However, from time 2 onwards, BW was 5.2 to 7.6% greater on the NP than on the HP diet but the differences were not statistically significant. Similarly, at times 2 and 4, fish on the NP diet had 14.8 to 17.2% greater DG, but the differences were not significant (Table 3). Growth displays such large variation within diets that the power of the statistical tests with 4 test tanks as replicates was not great enough to reach significance. Body lipid composition, in turn, was significantly greater on the NP diet, confirming that the diets significantly influenced components of growth (our unpublished observations).

In contrast to growth, both DFI and DFI percentage were greater, not lower, on the HP diet compared with the NP diet. At times 2 and 4, DFI was 39.3 and 23.3% greater on the HP diet, respectively ($P \leq 0.014$; Table 3). At time 3, the diet difference was lower (15.6%; $P = 0.16$). The difference between diets in DFI percentage was even greater than for the raw DFI (all $P \leq 0.054$), because of HP fish being smaller but feeding more than NP fish.

Variation on 2 Diets

The hypothesis of greater variation for growth on the alternative HP diet was not supported by the data. In contrast to the hypothesis, coefficients of phenotypic variation for BW were greater on the NP diet compared with the HP diet, and the difference was progressively increased from 3.7% at time 1 to 16.4% at time 5 (Table 4). Similarly, all CV_P of DG and 2 of 3 CV_P of DG percentage were greater on NP compared with HP diet.

Heritabilities for BW displayed only small differences between diets, the average heritabilities being 0.26 and 0.30 for NP and HP diets, respectively (Table 4). Heritabilities of BW were slightly smaller on the NP diet, even though the NP diet displayed greater phenotypic variation. This resulted from the fact that the residual variation was greater on the NP diet (average CV_R = 18.8) than on the HP diet (average CV_R = 16.7), whereas coefficients of additive genetic variation remained almost unaltered across the diets (average CV_A on NP = 11.1 and on HP = 11.0).

For DG, the average heritabilities were 0.37 on the NP and 0.29 on the HP diets, but with overlapping confidence limits (Table 4). The average CV_A for daily gain was 28.1 on NP and 21.9 on HP, showing that genetic variation was increased on the NP diet. The average CV_R was 34.9 on NP and 32.4 on HP diet. For DG percentage, average heritabilities were 0.31 and 0.25 on the NP and HP diets, respectively, and CV showed trends similar to raw DG (data not shown). Consequently, the hypothesis of increased variation on HP diet was not supported by daily gain data either; rather, if any trend was visible it was in contrast to our hypothesis.

For DFI, in 2 out of 3 cases, both CV_P and heritabilities were greater on the HP diet (Table 4). Average CV_P were 41.0 on the NP and 49.2 on the HP diet, showing increased phenotypic variation on the HP diet. Moreover, average heritability for DFI was 0.07 on NP and 0.13 on HP diet, and average CV_A was 10.4 on the NP and 17.0 on the HP diet, the values showing greater genetic variation on the HP diet. However, many of the heritabilities for DFI were small and not significantly different from zero. At the phenotypic level, DFI percentage showed increased variation on the HP diet (Table 4), whereas CV_A did not show great differences between the diets (data not shown).

Correlations Between Growth and Feed Intake

As hypothesized, growth traits and DFI were strongly correlated on the NP diet. On the NP diet, DG and DFI were strongly correlated at all sampling times (Table 5). The phenotypic and genetic correlations ranged from 0.51 to 0.74 and 0.86 to 0.96, respectively. Similarly, the phenotypic (0.48 to 0.54) and genetic correlations (0.72 to 0.90) between BW and DFI were all high on the NP diet.

On the HP diet, growth traits and DFI were uncoupled with successive time measurements (Table 5). At time 1 on the HP diet, growth traits and DFI were strongly correlated, as was the case for the NP diet. In contrast, at the later sampling times on the HP diet, the correlations between growth traits and DFI were reduced. At time 4 on the HP diet, the phenotypic correlations of DFI with BW and DG were 0.06 and 0.27, and the genetic correlations were –0.29 and 0.28, re-

Table 3. Sample sizes, means, and their SE for traits on 2 diets, and statistical tests for diet effect

		Normal protein			High protein			Statistical test for diet effect			
Trait[1]	Unit	n	Mean	SE	n	Mean	SE	df1[2]	df2[3]	*F*	*P*
BW_1	g	1,292	141	± 2.47	1,184	144	± 2.46	1	11.8	0.75	0.404
BW_2	g	983	770	± 16.7	1,096	724	± 16.6	1	7.19	4.12	0.081
BW_3	g	712	1,085	± 26.3	837	1,027	± 26.1	1	6.42	2.64	0.152
BW_4	g	621	2,167	± 53.7	700	2,059	± 53.3	1	6.16	2.12	0.195
BW_5	g	591	2,702	± 95.3	671	2,512	± 94.8	1	6.07	2.04	0.203
DG_1	g/d	671	3.13	± 0.197	660	3.17	± 0.197	1	6.31	0.02	0.890
DG_2	g/d	475	3.96	± 0.475	610	3.38	± 0.473	1	6.17	0.75	0.420
DG_4	g/d	406	17.8	± 2.00	486	15.5	± 2.00	1	5.99	0.65	0.452
$DG\%_1$	g/d	671	3.14	± 0.191	660	3.16	± 0.190	1	6.16	0.01	0.935
$DG\%_2$	g/d	475	3.83	± 0.489	610	3.52	± 0.487	1	6.12	0.20	0.669
$DG\%_4$	g/d	406	17.4	± 1.73	486	15.8	± 1.72	1	6.00	0.45	0.529
DFI_1[4]	g/d	639	1.45	–0.082	670	2.02	–0.096	1	6.77	20.3	0.003
				+0.084			+0.098				
DFI_2[4]	g/d	503	3.02	–0.204	583	3.49	–0.216	1	7.38	2.42	0.162
				+0.211			+0.223				
DFI_4[4]	g/d	405	13.3	–0.630	411	16.4	–0.706	1	6.64	10.9	0.014
				+0.645			+0.722				
$DFI\%_1$[4]	g/d	639	1.46	–0.084	670	2.01	–0.098	1	6.47	18.1	0.005
				+0.086			+0.100				
$DFI\%_2$[4]	g/d	503	2.89	–0.210	582	3.63	–0.233	1	6.97	5.35	0.054
				+0.218			+0.241				
$DFI\%_4$[4]	g/d	405	13.0	–0.602	411	16.7	–0.689	1	7.40	16.7	0.004
				+0.616			+0.704				

[1]DG = daily gain; DG% = relative daily gain; DFI = daily feed intake; and DFI% = relative daily feed intake. Five sampling times distributed between May 2002 and November 2003.
[2]df1 = nominator degrees of freedom for *F*-test given by the method of Kenward and Roger (1997).
[3]df2 = denominator degrees of freedom for *F*-test given by the method of Kenward and Roger (1997).
[4]Means and SE are back-transformed to the original scale after the analysis of square-root transformed values, giving different SE for lower (–) and upper (+) tails of the distribution.

Table 4. Phenotypic variances (σ^2_P), coefficients of phenotypic variation (CV_P), heritabilities (h^2), common environment ratios (c^2), and their SE for traits on 2 diets

	Normal protein						High protein					
Trait[1]	σ^2_P	CV_P	h^2	SE	c^2	SE	σ^2_P	CV_P	h^2	SE	c^2	SE
BW_1	1,237	28.0	0.33	0.15	0.32	0.08	1,168	27.0	0.36	0.16	0.32	0.09
BW_2	26,036	20.4	0.15	0.11	0.19	0.06	20,381	19.3	0.19	0.12	0.21	0.07
BW_3	53,087	21.2	0.38	0.13	0.07	0.05	39,192	19.2	0.36	0.14	0.19	0.07
BW_4	178,464	19.4	0.18	0.10	0.07	0.05	125,804	17.2	0.27	0.12	0.10	0.06
BW_5	308,552	20.6	0.26	0.10	0.03	0.05	195,152	17.7	0.31	0.12	0.07	0.05
DG_1	1.05	33.0	0.20	0.14	0.18	0.07	0.745	27.6	0.14	0.09	0.22	0.07
DG_2	6.19	66.3	0.49	0.11	—	—	3.52	55.3	0.40	0.10	—	—
DG_4	38.6	36.2	0.42	0.12	—	—	29.3	35.2	0.33	0.10	—	—
$DG\%_1$	0.556	24.0	0.24	0.11	0.04	0.05	0.390	20.0	0.17	0.09	0.09	0.06
$DG\%_2$	5.03	59.8	0.34	0.10	—	—	2.94	50.5	0.35	0.10	—	—
$DG\%_4$	27.2	30.4	0.36	0.12	—	—	22.3	30.7	0.23	0.10	—	—
DFI_1	0.295	37.5	0.03	0.06	0.15	0.06	0.383	29.9	0.14	0.10	0.18	0.07
DFI_2	2.08	44.5	0.17	0.10	—	—	5.07	59.3	0.06	0.07	—	—
DFI_4	33.5	41.1	0.02	0.07	—	—	112	58.5	0.19	0.11	—	—
$DFI\%_1$	0.202	31.1	0.14	0.09	0.06	0.05	0.182	20.6	0.17	0.10	0.06	0.05
$DFI\%_2$	1.60	39.0	0.09	0.07	—	—	4.62	56.6	0.05	0.06	—	—
$DFI\%_4$	25.8	36.1	0.06	0.08	—	—	110	58.0	0.00	0.05	—	—

[1]DG = daily gain; DG% = relative daily gain; DFI = daily feed intake; and DFI% = relative daily feed intake. Five sampling times distributed between May 2002 and November 2003.

Table 5. Phenotypic (above diagonal) and genetic (below diagonal ± SE) correlations between traits[1] on 2 diets

Diet	BW	DG	DFI
Normal protein, time 1			
BW		0.66	0.54
DG	0.84 ± 0.13		0.74
DFI	0.72 ± 0.26	0.95 ± 0.14	
Normal protein, time 2			
BW		0.43	0.49
DG	0.95 ± 0.09		0.56
DFI	0.90 ± 0.12	0.86 ± 0.11	
Normal protein, time 4			
BW		0.54	0.48
DG	0.92 ± 0.19		0.51
DFI	0.81 ± 0.58	0.96 ± 0.57	
High protein, time 1			
BW		0.69	0.72
DG	0.85 ± 0.08		0.73
DFI	0.89 ± 0.08	0.87 ± 0.08	
High protein, time 2			
BW		0.44	0.31
DG	0.84 ± 0.12		0.34
DFI	0.83 ± 0.42	0.76 ± 0.34	
High protein, time 4			
BW		0.49	0.06
DG	0.82 ± 0.13		0.27
DFI	–0.29 ± 0.30	0.28 ± 0.29	

[1]DG = daily gain; DFI = daily feed intake. Traits recorded at times 1 (May 2002), 2 (October 2002), and 4 (September 2003).

Table 6. Genetic correlations (r_A) and their SE between diets for traits

Trait[1]	r_A	SE
BW_1	0.96	0.05
BW_2	0.71	0.25
BW_3	0.91	0.11
BW_4	0.86	0.20
BW_5	0.93	0.13
DG_1	1.00	0.27
DG_2	0.98	0.09
DG_4	0.83	0.16
$DG\%_1$	1.00	0.23
$DG\%_2$	1.00	0.12
$DG\%_4$	0.69	0.24
DFI_1	0.99	0.76
DFI_2	0.08	0.55
DFI_4	0.84	1.34
$DFI\%_1$	0.71	0.32
$DFI\%_2$	–0.63	0.75
$DFI\%_4$	NE[2]	NE

[1]DG = daily gain; DG% = relative daily gain; DFI = daily feed intake; DFI% = relative daily feed intake. Five sampling times distributed between May 2002 and November 2003.
[2]NE = nonestimable due to low heritability.

spectively (Table 5). These correlations indicate better possibilities for simultaneous selection for high DG and against DFI on HP diet.

Genotype-by-Environment Interactions

Genetic correlations between the same measure recorded on both diets were estimated to investigate whether genetic improvement on one diet can be enhanced by selecting on an alternate diet (Falconer, 1952). Genetic correlations between the diets for BW were strong, above 0.71 (Table 6). Genetic correlation at time 2 was significantly different from unity, indicating a weak but existent genotype-by-environment interaction. For both DG and DG percentage, genetic correlations at times 1 and 2 were unity or close to it, whereas the correlations at time 4 differed from unity. Taken together, reranking of families for growth traits was only modest.

For DFI and DFI percentage, the between-diet correlations were lower than for BW (Table 6). At time 1, the correlations for DFI and DFI percentage were greater than 0.71. However, at time 2, the correlations were close to zero or negative. At time 4, estimation of the correlations between feed intake traits on both diets was problematic due to the low heritabilities, the correlations being either 0.84 with high standard error (DFI) or nonestimable (DFI percentage). These results demonstrate that feed intake was more prone to reranking than BW, especially at time 2.

Predicted Genetic Responses

Given the estimated genetic parameters, different selection strategies were assessed to analyze the way feed efficiency can be improved by selection for DG and against DFI, or by selection for DG only.

First, 2 sets of phenotypic and genetic (co)variance matrices for BW, DG, and DFI for market-sized fish (>700 g) were constructed, representing scenarios NP and HP. Because the standard errors of heritabilities for BW, DG, and DFI at times 2 and 4 were overlapping (Table 4), the means over both diets were used for both scenarios ($h^2_{BW} = 0.20$; $h^2_{DG} = 0.41$; $h^2_{DFI} = 0.11$). Because phenotypic variances, and phenotypic and genetic correlations between the traits were different in both diets, diet-specific estimates were used. The diet-specific mean estimates were obtained by calculating a mean estimate recorded at times 2 and 4.

Second, genetic gains in response to different selection strategies were predicted for DG and DFI by the standard selection index methodology for individual selection (Hazel, 1943; Cameron, 1997). Different selection strategies were assessed by switching step-by-step the relative economic weights from DG to DFI. A selection intensity of 1 was assumed. To calculate genetic response in feed efficiency, we first calculated mean feed efficiency (DG/DFI) in the base situation; that is, before selection (based on Table 3). Then, responses to selection were calculated for DG and DFI, and mean feed efficiency was recalculated.

The predicted genetic responses revealed that selection solely for rapid DG leads to a 17.6 to 18.6% increase in DG and simultaneously to 8.4 and 9.3% increases in

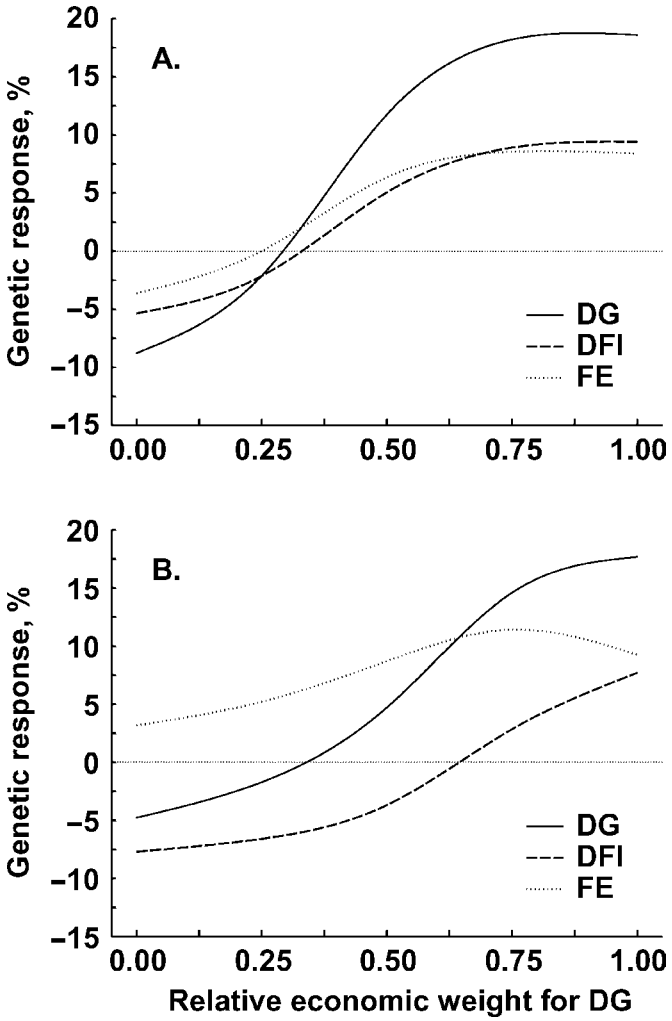

Figure 1. Predicted genetic responses (% of the mean before selection) in daily gain (DG), feed intake (DFI), and feed efficiency (FE) in normal protein (panel A) and high protein (panel B) scenarios after one generation of selection. The selection index includes DG and DFI, which are the 2 components of feed efficiency. The x-axis describes the relative economic weight given to DG. When x = 1, all economic weight is on DG; when x = 0.5, one-half of the weight is for DG and one-half is against DFI; and when x = 0, all weight is against DFI.

feed efficiency in both NP and HP scenarios, respectively (Figures 1A and B). This confirms that increasing DG was related to increasing feed efficiency, and that selection solely for DG will increase feed efficiency. A similar result was observed when BW was selected for (data not shown). When heritability of DFI is much lower than that of DG (Table 4), the latter responds much more rapidly to selection, leading to an automatic improvement in feed efficiency, even if the genetic correlation between the traits is high. It should be noted that the absolute levels of genetic gains are arbitrary and greater than expected to occur in reality (Kause et al., 2005).

In the NP scenario, the genetic response of feed efficiency was not increased by switching economic weight from selecting for DG to selecting against DFI (Figure 1A). The reason was the very strong unfavorable genetic correlation between DG and DFI, which hampers simultaneous breeding of the traits in opposite directions. However, in the HP scenario, the genetic response in feed efficiency was increased from 9.3 to 11.4% by selecting against DFI (–0.25 economic weight) and for DG (0.75 economic weight; Figure 1B). This was a result of the correlations between DG and DFI being only moderate, allowing simultaneous breeding of the traits in opposite directions.

DISCUSSION

Both feed costs and nutrient losses into the water from aquaculture can be reduced by improving the feed efficiency of fish. We showed here that selection solely for rapid daily gain could improve feed efficiency as a correlated genetic response. On the experimental diet, simultaneous selection for rapid DG and against DFI, in turn, may increase genetic gain in feed efficiency by a factor of 1.2 compared with selection solely for rapid DG. The results showed, however, that the variation for growth and feed intake and the relationships between the traits might differ in different nutritional environments, influencing genetic responses. Heritabilities and genetic correlations are indeed known to display environment-dependent variation (Falconer, 1952; Charmantier and Garant, 2005).

Diet Differences in Variation and Correlations

The current industrial on-growing diets for salmonid fish have high lipid (>35%) and low protein (<40%) contents. Such feeds are preferred because they support a high growth rate (but also increased lipid deposition), and the lipid component of feed is cheaper than the protein. Our results did not support the hypothesis of decreased variation in BW and DG on the modern NP diet. In contrast, phenotypic variation in growth was greater on the NP diet, and coefficients of genetic variation for DG were greater on the NP diet. No clear trend was seen for the heritabilities of the growth traits. The original hypothesis was based on a belief that the NP diet allows all fish to grow well, leading to low phenotypic variation in growth. The experimental HP diet, in turn, was hypothesized to be a challenge for fish with inefficient protein use, leading to their reduced growth, and thus, to increased variation in growth. Obviously these statements are incorrect, and they need to be replaced with an alternative hypothesis. For example, it is likely that variation in feed intake and growth is more a function of interactions between various nutrients (Hardy, 2002), rather than of the individual components, as hypothesized here.

In addition, we showed that both lipid and protein BW displayed greater phenotypic variation (CV_P) on the

NP diet compared with the HP diet (our unpublished observations). Thus, the increased phenotypic variation in wet BW on the NP diet was a result of both lipid and protein components of growth. Overall, the NP diet increased the expression of diverse BW, and depending on whether this resulted in an increase in residual or genetic variation, trait heritabilities were either reduced or elevated accordingly.

In contrast to the growth traits, DFI displayed greater phenotypic and genetic variation on the HP diet. After an initial reduction in variation on the HP diet just after the diets were applied, the variation in DFI in market-sized fish (times 2 and 4) was greater on the HP than on the NP diet. Moreover, as hypothesized, on the HP diet, growth and DFI were uncoupled as fish grew, whereas on the NP diet, growth and DFI were always strongly positively (unfavorably) correlated. The high positive phenotypic and genetic correlations of growth traits with DFI on NP diet indicate that the individuals with highest BW and DG fed the most. This was in agreement with studies on other farm animals [r_A between DG and DFI in beef cattle = 0.68, Koots et al. (1994); in lambs >0.7, Cammack et al. (2005); in pigs = 0.65, Clutter and Brascamp, (1998)], and results mostly from the fact that fish with greater growth feed more. It was not possible without further studies to reveal the mechanisms behind the diet differences in variation and correlations. Although speculative, it is possible that the greater consumption of a normal protein diet by faster growing fish may be partly due to their greater protein needs compared with slower growing fish (e.g., Houlihan et al., 1995). When protein content was high (HP diet), fast-growing fish required no extra feeding.

The greater DFI by the fast-growing fish on the NP diet results in greater intake of excess lipid, and consequently, exposes these fish to elevated deposition of lipid stores, as shown by the analysis of body and muscle composition (our unpublished observations). In contrast, for fish fed the HP diet, the genetic correlation between BW and lipid deposition was close to zero or negative, consistent with the diminished correlation between BW and DFI intake on that diet.

It may be argued that differential maturing of NP and HP fish could explain both the greater variation of feed intake and the uncoupling of growth and DFI on the HP diet. However, no support was found for this explanation. First, changing the fixed sex × maturity factor to sex or removing it totally from the statistical models increased phenotypic variation for DFI (and feed intake percentage) but the diet differences in CV_P were maintained (data not shown). Second, in the ANOVA results, the interaction of diet with sex × maturity was nonsignificant for all traits (data not shown), indicating that maturity process influenced the traits in a similar manner on both diets. Finally, phenotypic correlations of DFI with BW and DG for different sex × maturity classes remained low on the HP diet and high on the NP diet (data not shown); thus, maturity was not the cause of different correlations on the 2 diets.

Challenges in Genetic Analysis of Feed Efficiency in Fish

Restricted feeding may seem an appealing experimental treatment when studying feed efficiency. In farm animals, restricted feeding is used to reduce among-animal variation in feed intake. In this way, variation in growth is mostly a consequence of variation in feed efficiency, enhancing possibilities to improve feed efficiency by selection solely for rapid growth (Clutter and Brascamp, 1998). However, in socially structured fish populations such as rainbow trout, restricted feeding leads to increased dominance hierarchies, and thus, to strongly unequal distribution of feed within a population (McCarthy et al., 1992; Jobling, 1995; Jobling and Koskela, 1996). For instance, coefficient of phenotypic variation for feed intake under restricted feeding is greater than under satiation feeding in trout (McCarthy et al., 1992; Jobling and Koskela, 1996). Because of feed being unequally distributed between individuals during restricted feeding, it does not provide an efficient alternative to study feed efficiency in fish. Accordingly, when planning the current study, diets with different protein content were considered a more viable alternative.

Silverstein et al. (2001), working on catfish, were the first to report on individual feed intake in a family-structured fish population. They found a broad-sense heritability of 0.37 to 0.41 for feed intake. However, the majority of genetic studies on feed intake and feed efficiency in fish have been based on the average performance of full-sib families held in family tanks (Kinghorn, 1983; Thodesen et al., 2001; Doupé and Lymbery, 2004; Kolstad et al., 2004), which does not allow reliable estimation of genetic parameters. This results in elevating heritabilities because calculating tank means removes the large within-family variance from the data. Accordingly, we found an average heritability of 0.10 for DFI, whereas in the previous studies, heritabilities or proportion of variation due to family structure have been 0.31 to 0.84 (Kinghorn, 1983; Thodesen et al., 2001; Kolstad et al., 2004).

The weakness of our approach was the inaccuracy of the x-ray method to describe true long-term feed intake. This results from feed intake displaying large day-to-day variation (McCarthy et al., 1992; Jobling and Koskela, 1996), and thus, the correspondence between the short-term x-ray method and long-term recording was low (our unpublished observations). Moreover, the repeatability of DFI, even for the mean of 3 repeated records, was low to moderate, increasing residual variation. However, the x-ray method is the only method to record individual feed intake from large numbers of fish held in a common tank, and is routinely used for other fish species as well (McCarthy et al., 1993; Jobling et al., 2001; Silverstein et al., 2001).

Selection Strategies for Increasing Feed Efficiency

The analysis of predicted genetic responses in feed efficiency showed that selection solely for rapid growth improves feed efficiency as a correlated genetic response. This observation was in agreement with some (e.g., Thodesen et al., 1999; Ogata et al., 2002) but not all (Mambrini et al., 2004) fish studies examining correlated genetic changes in feed efficiency in response to selection for high BW, and with studies on fish and farm animals showing that growth and feed efficiency are favorably genetically correlated (Kinghorn, 1983; Koots et al., 1994; Clutter and Brascamp, 1998, Thodesen et al., 2001; Henryon et al., 2002; Doupé and Lymbery, 2004; Kolstad et al., 2004; Cammack et al., 2005).

Interestingly, in the NP scenario, the genetic gain in feed efficiency was not increased when DFI was selected against, along with selection for high DG. In contrast, on the HP diet, selection against DFI considerably increased genetic gain in feed efficiency. Moreover, a potentially realistic scenario was simulated in which heritability of DFI was artificially elevated to 0.25 for the HP scenario, all other estimates remaining the same as previously described. In this scenario, genetic response in feed efficiency was tripled by selecting against DFI. This scenario may be realistic because novel methods for recording feed intake in the future may increase the accuracy of records, thus elevating heritability values.

Great profits could be gained by improving feed efficiency through selection. Regardless of the intuitive benefits, none of the existing fish-breeding programs uses feed intake or feed efficiency in their selection index. Instead, they select for rapid growth or for high BW at a fixed age. The reason for the lack of selection efforts to improve feed efficiency is that individual feed intake is challenging and costly to record simultaneously from a large population of fish. Moreover, the favorable genetic correlation between BW and feed efficiency reduces the motivation to select directly for feed efficiency, although it could be advantageous.

Could an HP diet be used as a novel selection environment to improve feed efficiency on current commercial diets? In a seminal paper, Falconer (1952) concluded that to maximize a selection response, it is sometimes beneficial to select in an alternative environment, even when this environment is not a commercial production environment. Falconer (1952) showed that the greater the heritability in the alternative environment and the greater the genetic correlation between the environments, the more beneficial is the indirect selection in the alternative environment. In our study, DFI (and feed efficiency and residual feed intake, data not shown) displayed moderate reranking of families across the diets, suggesting that selection on the alternative HP diet does not lead to parallel changes on the commercial diet. Environment-specific expression of heritabilities and genetic correlations of feed intake and growth are utilized, for example, in pig breeding (Clutter and Brascamp, 1998). The present evidence, however, is not strong enough that such practice could be implemented in rainbow trout.

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