

A switch from fish- to plant-protein based feeds will not harm the current breeding program for European whitefish: Evidence from genetic analysis of feed utilisation traits

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Summary

A selective breeding program is currently under development that aims to enhance farmed European whitefish (*Coregonus lavaretus* L.), in order to increase aquafood supply chain productivity and consumer satisfaction in Finland. Critical steps in developing a breeding program are determining the amount of genetic variation in the population, and predicting how selection to change one trait may impact other traits. Diets for carnivorous fish currently contain protein mostly derived from wild fish sources. In order to reduce feed costs and environmental impact, alternative plant proteins have been researched for aquaculture diets. An issue of concern to the whitefish breeding program is the possibility of genotype by environment interaction (GxE), specifically that fish produced by the breeding program with the current diets may not perform well when they are reared with future plant-protein based diets. The aims of this study were (i) to assess whether sufficient genetic variation exists to improve growth, feed intake and feed efficiency on both types of diets through selection, and (ii) to predict whether selection on a fish meal (FM) based diet will lead to favourable correlated changes on a potential future soybean meal (SBM) based diet.

Seventy families were created from a series of factorial matings. Twenty-four individuals from each family were tagged and allocated to one of two diet treatments: a FM protein diet or a SBM protein diet. Individual weights were recorded at the beginning and end of the 3-month growth trial. During the trial, daily feed intake was measured 5 times per individual with X-radiography. Genetic parameters of final body weight, daily gain, daily feed intake, and feed efficiency were estimated with multiple-trait animal models.

Fish on the FM diet had faster growth, higher final weight, lower feed intake, and accordingly higher feed efficiency than those on the SBM diet. For both diets, daily gain showed the highest heritability ($h^2=0,20-0,40$), feed intake had lower h^2 ($0,17-0,23$), and feed efficiency and body weight had the lowest h^2 ($0,05-0,07$). Each trait appeared to show sufficient genetic variation for selective improvement for both diets. Daily gain and feed intake had high positive correlations (r_P and $r_A>0,86$) within both diets. Heritabilities were similar on both diets, and genetic correlations between the same traits recorded in each diet were very high ($r_A>0,92$). This indicates that little GxE exists for these traits, and selection to improve growth and feed utilization on the FM diet will have correlated improvement for the SBM diet.

In conclusion, the results of this study are favourable, and indicate that present selection to improve growth, feed intake, and feed efficiency within a FM-based diet will also improve the population for these traits within a SBM-based diet. Therefore, the improved population is likely to continue performing well as aquaculture diets move toward increased SBM protein contents.

Keywords

Whitefish, genetics, selection, breeding programs, genotype-environment interaction, fish feeds, soybean meal protein.

Introduction

A selective breeding program for European whitefish (*Coregonus lavaretus* L.) is currently under development in Finland. The program aims to enhance productivity in the entire aquafood supply chain and to increase consumer satisfaction by diversifying fish markets dominated by farmed rainbow trout and salmon. Growth and feed utilisation traits are of particular economic importance in this breeding program.

A critical step in developing a breeding program is estimation of genetic parameters such as heritabilities and correlations of important traits. Heritability is an estimate of the amount of genetic variation in a population, and predicts the rate of genetic progress that can be made from selective breeding. Genetic correlations estimate how selection to change one trait may impact other traits. At this time, no estimates of genetic parameters for whitefish growth and feed utilisation traits have been published in the scientific literature.

Currently, the major component of diets for carnivorous fish species such as whitefish is protein derived from wild fish sources. However, fish meal costs are rising and there is increasing concern about depletion of wild fish populations. Addition of proteins originating from plants to fish feeds is a way to reduce feed costs and environmental impact, and feed producers continue to increase the proportion of plant proteins in diets. Soybean products-based feeds are especially promising. In developing the breeding program, one issue of concern is the possibility of genotype by environment interaction (GxE), specifically that whitefish produced by the breeding program that are reared with the current fish meal protein-based diets may not perform well when they are reared with future plant-protein based diets. By calculating genetic parameters for growth and feed utilization under both types of diets, the effects of a future diet change on the breeding program can be predicted.

The aims of this study were (i) to assess whether sufficient genetic variation exists to improve growth, feed intake and feed efficiency through selection under both fish meal- and soybean meal-based diets, and (ii) to predict whether selection on a fish meal diet will lead to favourable correlated genetic changes on a potential future soybean meal diet.

Materials and Methods

Diets

Two experimental diets (fish meal and soybean meal) were formulated to contain equal amounts of protein (40%) and fat (21%). For the soybean meal diet, fish meal was substituted with soybean meal so that 50% of the protein was originated from soybean meal.

Experimental Design

The whitefish in the experiment originated from broodstock housed at the Finnish Game and Fisheries Research Institute's (FGFRI) Tervo Fisheries Research and Aquaculture station. A series of 2:2 factorial matings were done in October 2003 to create 70 full- and half-sib families descended from 52 dams and 43 sires. Family egg batches were incubated separately in running water. At the eyed-egg stage in January 2004, the families were transported to Laukaa Research Station of the FGFRI. From the time of hatching until the start of the experiment, each family was held in separate indoor tanks and reared at constant water temperature using commercial dry diets.

In June 2004, 24 randomly chosen individuals from each family were tagged. The fish were fed with a mixture of the experimental diets for four weeks before the initiation of the experiment in order to adapt them to the diets. There were six replicate experimental tanks per dietary treatment, so each tank contained two fish from each family.

During the trial, individual daily feed intake was measured every two weeks with X-radiography. With this technique, the feed was labelled with X-ray-dense markers, and the number of markers ingested by individual fish was counted from X-ray plates (Jobling *et al.*, 2001). The amount of feed eaten was calculated from this count. Five daily feed intake measurements were done on each fish in this manner. Individual average daily feed intake was calculated from these measurements.

Individual body weights were recorded at the beginning and end of the trial. Daily weight gain was calculated as the difference between initial and final body weights, divided by the number of days in the trial (77 to 80 d, depending on the tank). Individual feed efficiency was calculated as the ratio of

daily gain to average daily feed intake. Numbers of observations for each trait within the diets are shown in Table 1.

Statistical Analysis

Diet effects on final weight, daily gain, daily feed intake and feed efficiency were tested with analysis of variance, using the MIXED procedure in SAS 9.1 (SAS Institute Inc., Cary, NC, USA). The models included fixed effect of diet, and random effects of experimental tank, family, and diet by family interaction.

Phenotypic and genetic parameters were estimated with AI-REML using DMU6 (Madsen & Jensen, 2002). Final body weight, daily gain, feed intake, and feed efficiency were analysed with multiple-trait models. The models included the fixed effect of experimental tank, and random effects of family tank common environment, additive genetic, and residual error. Heritability (h^2) was the ratio of additive genetic variance to total phenotypic variance. Family tank common environment effect (c^2) was the ratio of family tank variance to total phenotypic variance. To obtain all correlations, a series of multiple-trait models were run with different trait combinations.

In order to examine genotype by environment interactions, observations recorded under each diet treatment were treated as separate traits (e.g. fish meal feed intake and soybean meal feed intake were defined as different traits). Therefore, the traits analysed were fish meal and soybean meal body weights, daily gains, daily feed intakes and feed efficiencies.

Results and Discussion

Diet Effects

At the start of the experiment, mean individual weight was $40,6 \pm 10,8$ g ($n=1647$) and there was no significant difference ($p=0,40$) between the dietary groups. At the end of the trial, whitefish on the fish meal diet had significantly higher final weight and daily gain, lower daily feed intake, and accordingly higher feed efficiency than fish fed the soybean meal diet (Table 1). This result was expected because the dietary value of soybean meal protein-based feeds are not yet as high as the value of traditional fish meal-based feeds. Furthermore, this confirmed that our experimental design was appropriate and influenced the fish as planned.

Table 1. Numbers of observations, least squares means \pm SE and diet test p-values for final body weight, daily gain, daily feed intake, and feed efficiency in fish meal and soybean meal diets.

| Trait | Fish meal | | Soybean Meal | | P |
|-------------------------|-----------|-------------------|--------------|-------------------|-------|
| | n | LS mean \pm SE | n | LS mean \pm SE | |
| Final Body Weight (g) | 765 | 131,2 \pm 2,34 | 768 | 125,8 \pm 2,34 | 0,013 |
| Daily Gain (g/d) | 765 | 1,145 \pm 0,021 | 768 | 1,090 \pm 0,021 | 0,001 |
| Daily Feed Intake (g/d) | 817 | 0,948 \pm 0,026 | 829 | 1,027 \pm 0,026 | 0,022 |
| Feed Efficiency | 765 | 1,208 \pm 0,020 | 768 | 1,078 \pm 0,020 | 0,001 |

Trait Heritability

Estimates of variances, heritabilities and family tank common environment effects are summarised in Table 2. In both diets, daily gain had the highest heritability (0,20 - 0,26), and daily feed intake had the second-highest heritability (0,17 - 0,23). Feed efficiency and final body weight showed the lowest heritability of the traits (0,05 - 0,07). The low heritability for body weight in both diets is an unusual result; in most studies weight traits show at least moderate heritability (Gjedrem, 2000). In this case, it appears that a large proportion of the variance was attributed to the family tank common environment; this is shown by the high common environment effect for body weight ($c^2 > 0,19$). However, when final body weight was adjusted for initial weight, as expressed by daily gain, or by adding a regression covariate for initial weight to the statistical model (results not shown) heritability results were higher, and more consistent with results of other studies. Generally, the heritability estimates predict that sufficient genetic variation exists for selective improvement of these traits in both diets.

Performances for all four traits tended to be more variable in the fish meal diet than in the soybean meal diet (shown by phenotypic variances and coefficients of variation). Similarly, traits measured under the fish meal diet tended to have slightly higher heritabilities than the same traits

measured under the soybean meal diet. Differences in growth and feed intake expression and heritability in different diet environments have also been found in rainbow trout (Kause et al., *in press*). However, the differences between diets in the current study are small and there is considerable overlap of standard errors. This suggests that response to selection may be slightly faster under the fish meal diet, but GxE is not likely to cause large differences.

Table 2. Phenotypic variances and coefficients of variation (CV), heritabilities (h^2) \pm SE, and family tank common environment effects (c^2) \pm SE for final body weights, daily gains, daily feed intakes and feed efficiencies measured in fish meal and soybean meal diet groups.

| Diet, Trait | Variance | CV | $h^2 \pm$ SE | $c^2 \pm$ SE |
|---------------------|----------|------|-----------------|-----------------|
| <i>Fish meal</i> | | | | |
| Final Body Weight | 1275,6 | 27,2 | 0,06 \pm 0,21 | 0,25 \pm 0,14 |
| Daily Gain | 0,134 | 31,9 | 0,26 \pm 0,18 | 0,13 \pm 0,09 |
| Daily Feed Intake | 0,095 | 32,5 | 0,23 \pm 0,15 | 0,08 \pm 0,07 |
| Feed Efficiency | 0,044 | 17,4 | 0,06 \pm 0,10 | 0,04 \pm 0,05 |
| <i>Soybean meal</i> | | | | |
| Final Body Weight | 948,0 | 24,4 | 0,05 \pm 0,19 | 0,19 \pm 0,12 |
| Daily Gain | 0,100 | 29,0 | 0,20 \pm 0,15 | 0,08 \pm 0,08 |
| Daily Feed Intake | 0,104 | 31,3 | 0,17 \pm 0,15 | 0,09 \pm 0,08 |
| Feed Efficiency | 0,033 | 16,9 | 0,07 \pm 0,11 | 0,07 \pm 0,06 |

Trait Correlations

Phenotypic correlations among body weight, daily gain, and daily feed intake within the fish meal and soybean meal diets were high and positive (Table 3). Therefore, fish with high body weight tended to be the ones that grew quickly and ate the most. Genetic correlations among these traits within each diet were also positive and very high (Table 3), although the low heritability of final body weight caused estimates involving this trait to have very high standard errors ($SE > 1,4$). Positive genetic correlations between growth and feed intake have also been found in rainbow trout (Kause et al., *in press*) and catfish (Silverstein et al., 2001).

The high genetic correlations indicate that animals with breeding values for high weight and fast gain also tended to have breeding values for increased feed intake. Therefore, selection to increase body weight will also cause faster gain and increased feed intake. The very high genetic correlation between daily gain and feed intake also indicates there will be very few fish with superior breeding values for both fast growth and low feed intake. Therefore, it may be difficult to simultaneously select for rapid growth and reduced feed intake in order to improve feed efficiency.

Table 3. Phenotypic (r_p) and additive genetic (r_A) \pm SE correlations between body weight, daily gain and daily feed intake within fish meal and soybean meal diets.

| Traits | Fish Meal | | Soybean Meal | |
|---------------------------|-----------|-----------------|--------------|-----------------|
| | r_p | $r_A \pm$ SE | r_p | $r_A \pm$ SE |
| Body Weight & Daily Gain | 0,97 | 0,88 \pm 2,15 | 0,96 | 0,85 \pm 1,41 |
| Body Weight & Feed Intake | 0,86 | 0,83 \pm 2,40 | 0,84 | 0,76 \pm 1,76 |
| Daily Gain & Feed Intake | 0,88 | 0,97 \pm 0,05 | 0,86 | 0,93 \pm 0,10 |

Genetic Correlations Between Diets

The extent of GxE was examined by estimating genetic correlations between a trait measured under the fish meal and the same trait measured under the soybean meal diet. These correlations indicate whether families have similar rankings within both the fish meal and soybean meal diet environments. Genetic correlations between the same traits recorded in each diet were all very high and positive. The genetic correlation between fish meal and soybean meal daily gains was $0,97 \pm 0,21$, and between average daily feed intakes was $0,93 \pm 0,28$. Estimates of genetic correlations between fish meal and soybean meal final body weights ($0,97 \pm 0,81$) and between feed efficiencies ($1,00 \pm 0,95$) were also very high, however the large standard errors associated with these correlations made these estimates inaccurate. As mentioned previously, these large errors were caused by the low heritability of these traits.

These genetic correlations indicate that the families ranked similarly across the diets and there is little genotype by environment interaction in this situation. If genetic selection is done to improve growth and feed utilisation under one diet, there will be a large correlated improvement for those traits under the other diet. Therefore, the fish that are selected under the current fish meal-based diets are likely to also be superior if the diet is changed in the future to a soybean meal-based diet.

Conclusions

In conclusion, the results of this study are favourable, and indicate that present selection to improve whitefish growth, feed intake, and feed efficiency within a fish meal-based diet will also improve the population for these traits within a soybean meal-based diet. Therefore, it is likely that the improved whitefish population will continue to perform well as aquaculture diets move toward increased plant protein contents.

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