

Quality and production trait genetics of farmed European whitefish, *Coregonus lavaretus*¹

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ABSTRACT: We present here phenotypic and genetic parameters for the major quality and production traits of farmed European whitefish. A total of 70 families were produced by mating each of 45 sires to an average of 1.6 dams and each of the 52 dams to an average of 1.3 sires. A total of 2,100 individuals were recorded for survival, and 507 individuals for growth and quality-related traits. The 4 major results were as follows: first, all traits exhibited nonzero heritabilities except for fillet gaping and fillet protein%. The heritabilities for the production traits were harvest weight (0.42 ± 0.10), gutted weight (0.40 ± 0.10), fillet weight (0.36 ± 0.09), maturity score (0.27 ± 0.11 , on liability scale), survival (0.19 ± 0.05 , on liability scale), carcass% (0.14 ± 0.07), and fillet% (0.11 ± 0.06). The heritabilities for the quality traits were condition factor (0.49 ± 0.10), fillet lipid% (0.37 ± 0.10), muscle texture (0.30 ± 0.09), Distell lipid reading (0.26 ± 0.09), fillet lightness (0.16 ± 0.07), fillet gaping (0.04 ± 0.06), and fillet protein% (0.04 ± 0.06). Second, the quality traits that were significantly genetically correlated with each other were all related to lipid deposition. Increasing fillet lipid% (an undesired change in whitefish) was genetically related

to desired lighter fillet color [genetic correlation (r_G) = 0.70 ± 0.22] and to undesired greater condition factor (0.39 ± 0.17). None of the other genetic correlations between condition factor, fillet lipid%, muscle texture, fillet lightness, fillet gaping, and fillet protein% were significant. Third, BW and gutted weight were genetically related to the quality traits that were genetically related to lipid deposition. Increasing harvest weight was genetically related to high fillet lipid% ($r_G = 0.59 \pm 0.14$), lighter fillet color (0.61 ± 0.25), and to greater condition factor (0.60 ± 0.12). All other genetic correlations of harvest weights with the quality traits were nonsignificant, indicating that rapid growth was not genetically related to gaping and softer flesh. Fourth, none of the genetic correlations of carcass%, fillet%, maturity, and survival with the quality traits were significant, implying weak genetic integration between the traits. Yet, marginally significant genetic correlations were found for fillet lipid% with maturity score ($r_G = -0.46 \pm 0.24$) and survival (0.36 ± 0.19). These results provide the genetic basis for assessing the potential to improve product quality via selective breeding.

Key words: aquaculture, heritability, lipid, quantitative genetics, selective breeding, survival

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INTRODUCTION

Selective breeding can be applied to improve product quality, but selection may also unintentionally reduce quality if unfavorable genetic correlations between production and quality traits exist. For 2 reasons, genetics of quality traits have been underrepresented in the farmed fish literature. First, production traits such as harvest weight and maturity age are usually easy to measure, so sufficient data for these can be collected when a breeding program is initiated (Gjerde and Schaeffer, 1989; Neira et al., 2004; Kause et al., 2005; Quinton et al., 2005; Powell et al., 2008). Second, fish breeding programs are typically focused on improv-

ing the profitability of primary production. Immediate costs and returns of product quality traits typically appear at the processor and retail levels, and thus product quality traits are easily neglected.

European whitefish *Coregonus lavaretus* (L.) is a white-fleshed carnivorous salmonid whose farming has recently began in Finland (Quinton et al., 2007a,b; Kause et al., 2009). In Finland, approximately 13 to 15 million kilograms of farmed fish are produced annually, of which nearly 10% is European whitefish. Here we present phenotypic and genetic parameters for the major production and product quality traits in European whitefish. The studied quality traits were fillet gaping, muscle texture, fillet lipid percentage recorded chemically and by Distell Fish Fat Meter, fillet protein%, fillet color lightness, and condition factor, and the studied production traits were harvest weight, gutted weight, carcass% of wet weight, fillet% of gutted weight, maturity age, and survival. The 4 topics of interest were to estimate 1) heritabilities for quality traits including fillet composition, fillet texture, fillet gaping, and color; and to estimate genetic correlations 2) between fillet lipid percentage and other quality traits, 3) between quality and growth, and 4) between quality and carcass and fillet yield, maturity, and survival.

MATERIALS AND METHODS

All procedures involving animals were approved by the animal care committee of the Finnish Game and Fisheries Research Institute (FGFRI).

The experimental fish originated from the recently established breeding program for European whitefish maintained at the Tervo station of the FGFRI located inland in mid-Finland (Quinton et al., 2007a,b). The progeny used here were produced at the Tervo station and transferred to brackish water in the Baltic Sea at the FGFRI Rymättylä Fisheries Research Station (60°19' N, 21°57' E) for grow-out and trait recording.

Population Structure

The analyzed population was created in October 30 to 31, 2003, at the Tervo station when 52 dams were crossed with 45 sires in a partial factorial design to produce 70 full- and half-sib families. Each sire was mated to an average of 1.6 dams and each dam to an average of 1.3 sires (both ranges 1 to 2). Sires and dams were assumed to be unrelated base population animals. These sires and dams were offspring of 50 males and 150 females collected from the wild (Kokemäki River, Finland) for which no pedigree information was available.

Rearing from eggs to fingerling tagging took place at Tervo. Families of fertilized eggs were incubated separately in funnels with running water. Eggs hatched in May 2004, after which the families were separately reared in 70 indoor 150-L family tanks. All families were fed to satiation using a feeding-robot (Arvo-Tec

Inc., Huutokoski, Finland). To ensure excess feeding, the feed amounts supplied were adjusted to be 1.3 times greater than predicted by the formulas of Koskela (1992).

Tagging was conducted over 6 wk in October to November 2004. At the start of tagging, there were a total of 7,417 fish, which were divided into 3 groups. For the first group, 40 fish per family were selected based on their large size (visually determined), tagged, and individually weighed. These largest fish were future breeding candidates and were kept at the Tervo breeding station to maximize genetic gain of growth in the nucleus population (Martinez et al., 2006). For the second group, 30 fish per family were tagged and held in a single tank before the transfer to the FG-FRI sea test station located in Rymättylä, South-West Finland, for production and quality trait recording of this study. These fish were roughly the next largest fish within the family. Thus, a total of 4,891 individuals (approximately 70 individuals per family) were tagged, and individual BW (g) of all these fish was recorded at tagging.

After the Tervo and Rymättylä groups of a family were tagged, the remaining fish from the family were counted (mean family size, $n_{\text{left}} = 36$ fish, range 12 to 105 per family), and their group BW (**Weightleft**) was recorded. This third group of leftover fish represented approximately the smallest fish in each family and was discarded. Individual records were generated for these remaining fish. Each of the n_{left} individuals in each family was assigned a tagging BW record equal to the mean of the family leftover mean BW ($\text{Weightleft}/n_{\text{left}}$).

The average BW at tagging of the fish held in Tervo, at sea, and of the leftovers were 47.3 g ($n = 2,793$), 45.6 g ($n = 2,100$), and 37.7 g ($n = 2,524$), respectively. Although only the traits recorded from the 2,100 sea-reared fish are reported in this study, tagging BW of all fish, either individually recorded or group means assigned for the culled individuals, were included as a trait in all multitrait genetic analyses to account for tagging preselection (Henderson, 1975; Pollak et al., 1984; Ouweltjes et al., 1988).

In April 2005, the 2,100 fish to be reared at the sea were vaccinated against furunculosis and vibriosis with Apoject injection (Koskela et al., 2004), and transported to the FGFRI Rymättylä Fisheries Research Station. Fish were randomly allocated over three 5- × 5- × 5-m net cages (C1, C2, C3). A large number of fish died during rearing, and therefore in May 2006, the fish from the C3 cage were randomly divided into cages C1 and C2. Fish were fed daily by computer-controlled feeding system (Itumic Inc., Jyskä, Finland) with Arvo-Tec feeders with commercial fish feed developed for whitefish according to the manufacturer's feeding tables and respective pellet sizes (Royal Silver, Raisio Feed Ltd., Raisio, Finland).

Three-summers-old whitefish were harvested from the sea cages between October to December 2006. The

Table 1. Trait units, sample sizes (n), trait means, phenotypic variances (V_p), coefficient of phenotypic variation (CV_p), and heritabilities ($h^2 \pm SE$) for production and quality traits

Trait	Unit	n	Mean	V_p	CV_p	h^2	SE
Production trait							
Tagging weight ¹	g	7,417	43.6	110.1	24.1	0.45	0.25
Harvest weight	g	507	995	52,398	22.9	0.42	0.10
Gutted weight	g	507	900	41,235	22.5	0.40	0.10
Fillet weight	g	507	563	17,996	23.7	0.36	0.09
Carcass%	%	507	90.7	4.1701	2.25	0.14	0.07
Fillet% of intact weight	%	507	56.4	7.0480	4.70	0.10	0.06
Fillet% of gutted weight	%	507	62.3	7.9616	4.53	0.11	0.06
Maturity score	Prop ²	507	0.36	0.1594	109	0.17	0.07
Maturity score						0.27 ³	0.11 ³
Survival	Prop	2,100	0.24	0.1763	174	0.10	0.03
Survival						0.19 ³	0.05 ³
Quality trait							
Fillet gaping	cm	507	1.33	2.2737	113	0.04	0.06
Fillet gaping score	Prop	507	0.54	0.2379	89.9	0.01	0.06
Fillet gaping score						0.02 ³	0.09 ³
Muscle texture	N/cm ²	507	0.027	5.044×10^{-5}	26.8	0.30	0.09
Fillet lipid%	%	498	12.2	10.454	26.4	0.37	0.10
Distell lipid	Relative scale 0 to 100	369	53.4	45.356	12.5	0.26	0.09
Fillet protein%	%	503	19.3	1.0136	5.20	0.04	0.06
Fillet lightness	Gray scale 0 to 100	505	42.6	5.8204	5.67	0.16	0.07
Condition factor	g/cm ³	507	1.71	0.0623	14.6	0.49	0.10

¹ $c^2 = 0.26 \pm 0.14$. c^2 = full-sib-family variance/phenotypic variance.

²Prop = proportion of mature fish or broken fillets.

³ $h^2 \pm SE$ calculated on the liability scale following Dempster and Lerner (1950).

fish from the first cage were slaughtered in 5 groups over 2 d, and the fish from the second cage were slaughtered in 4 groups over 2 d. Slaughter group within each sea cage indicates fish that were killed and recorded together (i.e., that share common management). All traits analyzed here were recorded at harvest (i.e., after 1 growing season in fresh water and 2 seasons in brackish seawater).

Traits Analyzed: Production Traits

The harvest traits analyzed and reported here were recorded from the 2,100 tagged fish sent to the sea. Production traits refer here to traits that mainly influence quantity of fish production and products, whereas quality traits influence the value of fish and fish products. All trait definitions were adapted to fit commercial practices. The preferred directions of trait changes are based on the expected improvements in a supply chain profit (farmers, processor, retail; Kankainen et al., 2007). At harvest, 6 production traits were recorded: harvest weight, gutted weight, carcass percentage, fillet percentage, maturity score, and survival (Table 1).

At harvest, all fish were measured for wet harvest weight (to the nearest gram) and then eviscerated, and gutted weight was recorded (n = 507 fish). Carcass percentage was calculated as $\text{carcass}\% = 100 \times (\text{gutted weight}/\text{harvest weight})$. For each individual, the 2 fillets were cut, lipid deposits from belly flaps and around fins were removed, and the remaining fillets with the

skin on were weighed (g). The fish were filleted by a technician with professional qualifications from an industrial processing plant. Fillet percentage was calculated as $\text{fillet}\% = 100 \times (\text{fillet weights}/\text{gutted weight})$. Maturity score was defined as 1 = mature fish or 0 = immature. Gonad percentage [$100 \times (\text{gonad weight}/\text{harvest weight})$] ranged from 0 to 20.2%, and a fish was determined mature if its gonad percentage was greater than 2%. Four maturity-sex categories were defined as mature males (n = 163 fish), immature males (n = 100), mature females (n = 22), and immature females (n = 222). The fish had normal external appearance and grew at the expected rate. However, during filleting when the skeleton becomes visible, it was observed that in many fish (52.7%) 2 to 3 vertebrae were compressed, forming a small hump. Spines of all fish were visually scored as 1 = affected or 0 = normal, and this was used as a fixed factor in the statistical models. For instance, compared with normal fish, the affected fish had greater condition factor (1.80 vs. 1.63; $P < 0.001$), less carcass% (81.1 vs. 84.2%; $P < 0.001$), and less fillet% of gutted weight (61.5 vs. 62.6%; $P < 0.001$), and their final harvest weight differed (965 vs. 1,017 g; $P = 0.01$). Survival was defined as survival from tagging to harvest as 1 = survived or 0 = tag of the individual not present at harvest. All 70 families were still represented at the end of the experiment.

It should be noted that viscera% ($100 - \text{carcass}\%$) is the reverse of carcass%. In rainbow trout, viscera percentage is a reliable indicator trait of visceral lipid (Tobin et al., 2006; Kauser et al., 2007a). Thus, some of

the carcass% correlations are better understood when interpreted as correlations of the lipid-related trait viscera% (with reversed signs of the correlations).

Traits Analyzed: Quality Traits

Six quality traits were recorded: fillet gaping, muscle texture, fillet lipid percentage, fillet protein percentage, fillet color lightness, and condition factor (Table 1).

Fillet color lightness was measured from epaxial muscle at 3 locations along a fillet with a Minolta spectrophotometer (model 2600d, Tokyo, Japan), according to the CIE $L^*a^*b^*$ method (CIELAB). Each measurement was run in triplicates [i.e., 3 flashes of daylight (D65, observer angle 10°) per site were performed]. Lightness (L^*) describes the gray color scale from black (smallest value) to white (largest value). Greater lightness is the desirable phenotype in whitefish filets. Fillet gaping (in centimeters) was defined as the total length of flesh gaping (separation of myotomes) on the dorsal part of a fillet. Filets were laid flat, and the length of the area containing gaping above lateral line was measured with a ruler.

Because the frequency distribution of gaping was skewed with a long right-hand tail, gaping was also scored as a binary trait (1 = gaping occurred, 0 = no gaping) and its heritability estimated on the underlying liability scale following Dempster and Lerner (1950). This practice functions as a general normalizing transformation for strongly nonnormal distributions (Roff, 2001). To record muscle texture, a 4-cm square shaped piece of white muscle was cut from epaxial postrigor muscle. A TA.XTPplus texture analyzer (Stable Micro Systems Ltd., Inverness, UK) with Warner-Bratzler knife (HDP/WBV, Stable Micro Systems Ltd.) was used to cut through the sample. The trigger force was 0.1 N, and the speed of the blade before, during, and after the test was set to 2 mm/s, 2 mm/s, and 10 mm/s, respectively. The maximum force (in newtons) required to cut the sample was recorded. After the test, the cut surface of the sample was scanned (Canon, CanonScan 3200F, Lake Success, NY) and areas were calculated using image analysis software (Image J, 1.37v, National Institute of Mental Health, Bethesda, MD). Texture (N/mm^2) was calculated as texture = force/sample surface area. Because over-firm texture is not observed in whitefish filets, high texture value (i.e., firm fillet) is the desirable phenotype.

To measure proximate fillet composition, one skinned, trimmed fillet from each individual was frozen, and composition determined as described by Elvingsson and Sjauna (1992) and Tobin et al. (2006). In brief, a fillet was minced and a subsample of 10 g was homogenized in standard solvent (Mirasolve, Miris AB, Uppsala, Sweden) to analyze fillet lipid and protein percentages by mid-infrared transmission spectroscopy using a FMA2001 Milk Analyzer (Miris AB). Two analyses were conducted on each sample. The individual record used in the statistical analyses was a mean of

these 2 analyses. Extensive lipid deposition should be avoided, and increased protein% is a desired characteristic. Condition factor was calculated from harvest weight (in grams) and body length (millimeters) as follows: condition factor = $100 \times (\text{harvest weight}/\text{body length}^3)$. Low condition factor represents a desirable slender shape, whereas larger values represent an undesirable round or deep shape (Kause et al., 2003, 2004).

Traits Analyzed: Distell Fish Fat Meter Records

Distell Fish Fat Meter readings were only taken on the first 380 harvested fish. Readings were taken on the intact fish (before gutting) 4 times per fish from the head toward the tail, just above the lateral line on the left side of a fish. The raw Distell readings obtained by so-called research calibration (values 1 to 100) were used in the analysis without transforming them to estimates of lipid percentages.

Repeatability of the 4 Distell readings was 0.59, indicating moderate consistency for the repeated records. Less than unity repeatability here may be both due to recording error and a true change in the ranking of individuals when lipid is recorded from head toward tail. In our genetic analysis, the mean of the 4 recordings for each individual was used. The repeatability of the mean of the 4 recordings was 0.85 (calculated following Kause et al., 2006), revealing greater accuracy when the mean is calculated for each individual. The accuracy for the mean was greater than for the original raw records because the mean contains a greater amount of information than a single raw observation.

Genetic Analysis

Phenotypic and genetic parameters were estimated using 3-trait animal models with DMU6 software, applying average information REML methods (Madsen and Jensen, 2008). Pedigree included sires, dams, and their offspring. Full correlation matrices between all traits were obtained using a series of multitrait runs with 3 traits each. Each 3-trait analysis contained tagging BW in the model to account for the selection that occurred at tagging. The impact of such selection bias on the genetic parameter estimates can be reduced by running a multitrait analysis with the selected trait(s) included (Henderson, 1975; Pollak et al., 1984; Ouweltjes et al., 1988). The statistical models used for different traits are given in Table 2. The impact of the fixed effects on the traits was assessed using Proc Mixed (SAS Inst. Inc., Cary, NC), and the factors contributing to the trait variation (with $P < 0.1$) were included in the genetic analysis.

A simulation was conducted to assess the degree to which tagging weight variation within a family is reduced when the group mean is used for the culled animals of the family. A normally distributed trait with CV of 25 and mean of 43.6 g was simulated. The results

showed that if 34% of individuals are culled (as in our data), the variance is reduced to 91% of the original full variance. In our data, few extreme families had either 15 or 48% individuals culled, corresponding to 97 to 86% reduction in the variance, respectively. Thus, the use of group mean for the culled individuals may induce some small changes to heritabilities and residual correlations, but the effects are likely to be only moderate. The simulation produces the worst-case scenario because strict threshold culling was simulated, but in reality the workers were removing fish by hand based on appearance. Thus, a greater proportion of variance remains within a family. Heritabilities of the traits not correlated with tagging weight should not be influenced by the use of the group mean. The reason for the rather stable family sizes at tagging is that family sizes were standardized (no grading or selection) during very early growth.

Gaping score, maturity score, and survival are binary traits, and therefore their heritabilities and SE were transformed to the underlying liability scale following Dempster and Lerner (1950). Phenotypic correlations for binary traits calculated using a linear model are typically underestimates, whereas genetic correlations are unbiased (Mäntysaari et al., 1991).

When calculating correlations for maturity score, the fixed maturity effect was dropped from the models of the other traits in the same multiple-trait model. For survival, there are no phenotypic and residual correlations determined in the models with other traits except tagging weight because all individuals that died lack observations for the other traits. Genetic correlations were considered significant or marginally significant when $r_G \pm (1.96 \times SE)$ or $r_G \pm (1.64 \times SE)$ did not include zero, respectively.

RESULTS

Heritability

The traits with heritability of 0.30 or greater were tagging weight, harvest weight, gutted weight, fillet weight, texture, fillet lipid%, and condition factor (Table 1). The traits with heritability between 0.15 to 0.30 were maturity score, survival (on liability scale), Distell lipid reading, and fillet lightness. The traits with heritability less than 0.15 were carcass%, fillet%, fillet gapping, and fillet protein%. Heritabilities of gapping and protein% were close to zero (≤ 0.04), and their SE were greater than the heritability estimates (Table 1).

Correlations Between Quality Traits

Only 2 out of 15 genetic correlations between the quality traits were significant, revealing that the quality traits were not strongly genetically integrated (Table 3). Fillet gapping was not significantly phenotypically correlated with any other quality trait. The genetic correlations of fillet gapping with other quality traits had

Table 2. Factors¹ used in the statistical models to estimate (co)variance components

Trait	Random			Fixed				Covariate		
	Anim _i	Fullsib _j	Cage _k	Sgroup _l	Matsex _m	Sex _n	Verte _o	βTempSum	βLength	
Tagging weight	×				×					
Harvest weight, gutted weight, fillet weight, carcass%, fillet%, texture, lipid%, Distell lipid, protein%, lightness, condition factor	×	×	×	×	×		×	×		
Fillet gapping	×				×		×		×	
Maturity score	×									
Survival	×					×				

¹Model terms are as follows: Anim_i = random genetic effect for individual i (i = 1-number of individuals); Fullsib_j = random effect for full-sib family j modeled without pedigree information (j = 1 to 70). Full-sib effect (c^2 = full-sib-family variance/phenotypic variance) was negligible ($c^2 \leq 0.02$) for all other traits than tagging weight; Cage_k = fixed effect of sea cage combination k (k = 1 to 4); Sgroup_l = fixed effect of slaughter group l (l = 1 to 9); Matsex_m = fixed effect of combined maturity-sex category m (m = 1 to 4); Sex_n = fixed effect of sex n (n = 1 to 2); Verte_o = fixed effect of vertebrae defect category o (o = 1 to 2); βTempSum = fixed covariate for cumulative degree-days at tagging; βLength = fixed covariate for body length at slaughter.

Table 3. Phenotypic correlations (above the diagonal) and genetic correlations (below the diagonal; \pm SE) between quality traits¹

Item	Fillet gaping	Muscle texture	Fillet lipid%	Fillet protein%	Fillet lightness	Condition factor
Fillet gaping	—	-0.02	0.08	-0.03	0.00	0.11
Muscle texture	ne	—	-0.32	-0.13	0.16	-0.31
Fillet lipid%	ne	-0.23 \pm 0.21	—	-0.07	0.15	0.42
Fillet protein%	ne	ne	ne	—	-0.26	0.10
Fillet lightness	ne	-0.10 \pm 0.29	0.70 \pm 0.22*	ne	—	0.01
Condition factor	ne	-0.31 \pm 0.19	0.39 \pm 0.17*	ne	0.34 \pm 0.25	—

¹ne = nonestimable due to close-to-zero heritability.

*Confidence limit ($1.96 \times$ SE) does not include zero.

very large SE and were nonestimable (Table 3), which was caused by the low heritability of gaping (Table 1).

None of the genetic correlations with texture were significant (Table 3). At the phenotypic level, increasing texture (tougher muscle) was related to decreasing fillet lipid% and condition factor. This is logical because lipid% and condition factor were positively correlated, possibly because high lipid deposition leads to round body shape (Table 3).

Increasing fillet lipid% (unfavorable change) was phenotypically and genetically related to increasing fillet lightness (favorable change; Table 3). Genetic correlations of lipid% with gaping and texture were nonsignificant or nonestimable. Yet, at the phenotypic level, increasing lipid% was related to decreasing texture (softer fillet). Fillet lipid% had favorable positive phenotypic and genetic correlations with condition factor, indicating that a desirable lesser condition factor (slender shape) was favorably associated with less lipid% (Table 3).

Genetic correlations of fillet protein% with other quality traits were nonestimable due to close-to-zero heritability for protein% (Table 3). At the phenotypic level, increasing protein% was related to decreasing lightness (darker fillet). This is opposite to fillet lipid% (Table 3).

The mean Distell lipid readings had high positive phenotypic and genetic correlations with the chemically determined fillet lipid% ($r_P = 0.74$, $r_G = 0.84 \pm 0.09$, respectively). Accordingly, the correlations of Distell records with the production and quality traits were similar to those of fillet lipid% (no results shown).

Correlations Between Quality and BW

Six out of the 12 genetic correlations of the quality traits with either BW or gutted weights were significant (2 favorable, 4 unfavorable; Table 4). As expected from the work on rainbow trout (Kause et al., 2007c), harvest and gutted weights had unfavorable positive phenotypic and genetic correlations with fillet lipid% and condition factor. Harvest weight and gutted weight had favorable positive genetic correlations with fillet lightness (but zero phenotypic correlations), which indicates that selection for increased harvest weight will also cause desirable lighter fillet color. This may, how-

ever, be a side effect of greater lipid content in these fish because fillet lipid% and fillet lightness were highly positively genetically correlated (Table 3). Fillet weight displayed similar correlations with quality traits as gutted weight (Table 4) because fillet and gutted weight have a close-to-unity correlation (Table 5).

All other genetic correlations of harvest and gutted weights with quality traits were nonsignificant. However, there were noticeable relationships between the traits at the phenotypic level. At the phenotypic level, increasing harvest weight was unfavorably related to high gaping and low texture (soft muscle). At the genetic level, these relationships were nonsignificant. Phenotypic correlations of tagging weight with the quality traits were low (from -0.08 to 0.16), and none of the respective genetic correlations were significant (Table 4).

Correlations Between Quality and Carcass%

All the genetic correlations of carcass% with the quality traits were nonsignificant (Table 4). At the phenotypic level, reduced carcass% (and thus greater viscera%) was related to high fillet lipid% and greater condition factor (Table 4), indicating that viscera% is a lipid-related trait.

Correlations Between Quality and Fillet%

None of the genetic correlations of fillet% with the quality traits were significant (Table 4). At the phenotypic level, moderate relationships were noted. Greater fillet% was phenotypically favorably related to greater fillet protein%, and unfavorably related to reduced texture (softer fillet), increased fillet lipid%, less fillet lightness (darker fillet), and greater condition factor (round shape; Table 4). The reader should note that greater condition factor was phenotypically and genetically related to greater fillet lipid% (Table 3) and phenotypically also to greater fillet%.

Correlations Between Quality and Maturity Score

Of the 6 correlations of maturity score with quality traits, only fillet lipid% was marginally significant

(Table 4). Maturity score had a negative genetic correlation with fillet lipid%, showing that early maturing fish had less fillet lipid%. This result is logical because maturity effect on lipid% was not accounted for when calculating the correlation and the maturing fish had initiated gonad development, decreasing fillet lipid%.

At the phenotypic level, maturity score had positive phenotypic correlations with texture and fillet lightness. Therefore, mature fish tended to have fillets with lighter color and firmer texture.

Correlations Between Quality and Survival

The genetic correlation between lipid% and survival was positive and marginally significant, implying that greater lipid% may be genetically related to greater survival (Table 4). All other genetic correlations of survival with quality were nonsignificant, implying weak relationships between the traits.

Correlations Between Production Traits

Tagging weight, harvest weight, gutted weight, and fillet weight were highly positively correlated with the correlations being about 1 (Table 5). Increasing harvest weight was phenotypically and genetically related to decreasing carcass% (and thus to increasing viscera%). This unfavorable relationship was weaker for gutted weight, as shown by the decreased phenotypic correlation and the nonsignificant genetic correlation.

Increasing BW and gutted weights were phenotypically related to increasing fillet%. The respective genetic correlations were weak, but for gutted weight marginally significant and again more favorable than for intact harvest weight. All other genetic correlations of harvest and gutted weights with production traits were nonsignificant.

Early maturity was phenotypically and genetically related to decreased carcass% (and thus increased viscera%; Table 5). Survival was nonsignificantly correlated with other production traits.

DISCUSSION

The 4 major results of the present study were as follows. 1) All traits exhibited nonzero heritabilities except for fillet gaping and fillet protein%. 2) The quality traits that were significantly genetically correlated with each other were all related to lipid deposition (fillet lipid%, fillet lightness, and condition factor). All other genetic correlations between the quality traits were nonsignificant, indicating that fillet lipid% is not genetically related to texture or gaping. 3) Body, gutted, and fillet weight were genetically related to the 3 quality traits that were genetically related to lipid deposition (fillet lipid%, fillet lightness, and condition factor). All other genetic correlations of harvest weight with the quality traits were nonsignificant, indicating that rapid growth is not genetically related to gaping and softer

Table 4. Phenotypic correlations (r_p) and genetic correlations ($r_G \pm SE$) between production and quality traits¹

Trait	Fillet gaping		Muscle texture		Fillet lipid%		Fillet protein%		Fillet lightness		Condition factor	
	r_p	$r_G \pm SE$	r_p	$r_G \pm SE$	r_p	$r_G \pm SE$	r_p	$r_G \pm SE$	r_p	$r_G \pm SE$	r_p	$r_G \pm SE$
Tagging weight	0.02	ne	-0.01	-0.13 ± 0.31	0.12	0.40 ± 0.33	-0.08	ne	0.07	0.89 ± 0.85	0.16	0.29 ± 0.19
Harvest weight	0.18	ne	-0.26	-0.10 ± 0.22	0.55	0.59 ± 0.14*	0.11	ne	0.00	0.61 ± 0.25*	0.65	0.60 ± 0.12*
Gutted weight	0.20	ne	-0.26	-0.13 ± 0.21	0.55	0.60 ± 0.14*	0.12	ne	-0.01	0.58 ± 0.25*	0.64	0.60 ± 0.13*
Fillet weight	0.21	ne	-0.27	-0.13 ± 0.24	0.55	0.59 ± 0.14*	0.15	ne	-0.02	0.61 ± 0.26*	0.63	0.61 ± 0.13*
Carcass%	0.01	ne	0.09	-0.39 ± 0.28	-0.19	-0.15 ± 0.27	0.03	ne	-0.03	-0.48 ± 0.32	-0.27	-0.16 ± 0.25
Fillet% of gutted weight	0.09	ne	-0.23	-0.29 ± 0.29	0.24	-0.04 ± 0.30	0.22	ne	-0.14	0.14 ± 0.41	0.23	0.22 ± 0.27
Maturity score	-0.03	ne	0.18	0.14 ± 0.27	-0.01	-0.46 ± 0.24	-0.04	ne	0.17	-0.41 ± 0.32	-0.04	0.06 ± 0.25
Survival ²	ne	ne	ne	-0.09 ± 0.21	ne	0.36 ± 0.19	ne	ne	ne	-0.11 ± 0.24	ne	0.16 ± 0.24

¹ne = nonestimable due to close-to-zero heritability.

²Only genetic correlations can be calculated between survival and traits at harvest.

*Confidence limit ($1.96 \times SE$) does not include zero.

flesh. 4) The quality traits were weakly genetically related to carcass%, fillet%, maturity, and survival. All in all, these results provide the genetic basis for assessing the potential to improve product quality via selective breeding, and the results should be combined with economic values to yield an optimal selection strategy.

Considering that the genetic parameters were estimated with a population that experienced preselection, was affected by mild vertebrae defects, and had greater mortality, a reader should be prudent when extrapolating the results.

Gaping and Texture

In European whitefish, 2% of the fish are downgraded due to gaping and soft fillet (Kankainen et al., 2007). In our study, heritability for texture was moderate [heritability (h^2) = 0.30], allowing its genetic improvement by selection. Neira et al. (2004) estimated heritability of 0.06 and 0.09 for texture in Coho salmon (*Oncorhynchus kisutch*). Heritability of texture can be easily influenced by recording technique, potentially generating variation between studies.

In contrast to texture, fillet gaping in European whitefish was mainly determined by nongenetic factors ($h^2 = 0.04$), and it was neither phenotypically nor genetically related to any other trait. Thus, it is unlikely that selective breeding can be used to reduce fillet gaping. Gaping is considered to be a postmortem phenomenon (Michie, 2001). Decreased meat pH, caused by breakdown of glycogen during slaughter, contributes to gaping, and gaping is influenced by slaughter and storage methods (Rasmussen, 2001; Mørkøre et al., 2002; Kiessling et al., 2004). European whitefish in particular requires gentle primary processing (S. Airaksinen, personal observation).

We found no genetic relationships for lipid% with gaping and texture, providing no evidence that texture and gaping should change as a correlated genetic response to increased lipid deposition. Similarly, in Coho salmon, muscle lipid% and visceral lipid% had nonsignificant genetic correlations with texture (Neira et al., 2004).

At the phenotypic level, however, increasing fillet lipid% was related to reducing fillet texture (i.e., to softer fillet). Similar to our study, Mørkøre et al. (2002) found a negative correlation between fillet lipid content and fillet firmness in Atlantic salmon, but Johnston et al. (2007) found strong negative, weak negative, or no correlation between fillet firmness and cutlet lipid% in a series of experiments with Atlantic salmon. Neira et al. (2004) found consistently that texture was not correlated with muscle lipid% and visceral lipid% in Coho salmon ($r_p = -0.06-0.02$). In our study, decreasing texture (softer muscle) was phenotypically related to both increasing fillet lipid% and increasing condition factor. That both fillet lipid% and condition factor showed a similar result is logical because high lipid deposition was related to round body shape.

Table 5. Phenotypic correlations (r_p , above the diagonal) and genetic correlations (r_G , below the diagonal; \pm SE) between production traits¹

Item	Tagging weight	Harvest weight	Gutted weight	Fillet weight	Carcass%	Fillet% of gutted weight	Maturity score	Survival
Tagging weight	—							
Harvest weight	0.63 \pm 0.17*	0.34		0.31	-0.02	0.00	0.21	-0.21
Gutted weight	0.61 \pm 0.20*	—	0.32	0.99	-0.28	0.33	0.07	ne
Fillet weight	0.60 \pm 0.25*	1.00 \pm 0.00*	—	0.99	-0.17	0.36	0.03	ne
Carcass%	-0.13 \pm 0.38	1.00 \pm 0.00*	0.99 \pm 0.00*	—	-0.19	0.48	0.02	ne
Fillet% of gutted weight	-0.28 \pm 0.42	-0.48 \pm 0.22*	-0.16 \pm 0.25	-0.46 \pm 0.24	—	-0.18 ¹	-0.43	ne
Maturity score	0.35 \pm 0.32	0.03 \pm 0.29	0.29 \pm 0.16	0.42 \pm 0.22	-0.26 \pm 0.36 ²	—	-0.04	ne
Survival	0.29 \pm 0.28	0.12 \pm 0.25	-0.07 \pm 0.26	-0.02 \pm 0.26	-0.79 \pm 0.16*	0.46 \pm 0.34	—	ne
		0.31 \pm 0.18	0.31 \pm 0.18	0.29 \pm 0.19	-0.30 \pm 0.25	-0.10 \pm 0.28	0.16 \pm 0.24	—

¹ne = nonestimable.

²When fillet% is expressed as a percentage of intact harvest weight, $r_G = 0.31 \pm 0.35$ and $r_p = 0.31$.

*Confidence limit ($1.96 \times SE$) does not include zero.

Reduced texture is known to be influenced by reduced cross-linking in collagen and by increased meat pH (e.g., during cooking), and it is affected by storage and slaughter methods (Love, 1980; Rasmussen, 2001; Mørkøre et al., 2002; Kiessling et al., 2004). Although texture and gaping are partly determined by similar mechanisms (Rasmussen, 2001), they were not phenotypically correlated in European whitefish.

Fillet Lipid and Protein Percentage

The aim of farmed fish production is to convert feed into muscle and ultimately protein growth rather than excess lipid and slaughter waste. Hence, the genetic improvement of fillet and body protein percentage should be of high priority for breeders, but this is challenging in practice. In line with the previous literature (Tobin et al., 2006; Kause et al., 2009), heritability for fillet protein% in European whitefish did not differ significantly from 0 ($h^2 = 0.04$). In salmonids, body and fillet protein shows limited variation across different diets, rearing treatments (Austreng and Krogdahl, 1987; Shearer, 1994), and families, preventing effective breeding efforts (Tobin et al., 2006; Kause et al., 2009). Such homeostasis may be maintained by varying feed intake and deposition of protein to obtain certain target protein% levels (Ruohonen et al., 2007).

Fillet protein% was phenotypically related to darker fillet color. The same was observed in Arctic char (*Salvelinus alpinus*) by Hatlen et al. (1998) and in rainbow trout by Kause et al. (2008). This is a likely result because protein-rich muscle fibers are gray in European whitefish. Compared with lipid traits, the correlation estimates of protein% with product quality are under-represented in the literature because the lack of variability in protein traits seems to have reduced the interest of researchers (Kause et al., 2009).

In the present study, heritability for chemically determined fillet lipid% was 0.37, allowing effective selection efforts. In contrast to fillet protein%, mechanisms holding body and fillet lipid percentage invariable within a population are weaker in salmonids (Kause et al., 2009). This explains the observations that cascades of lipid deposition can occur during fish growth, leading to greater amounts of phenotypic and genetic variation for percentage body and fillet lipid (Gjedrem, 1997; Tobin et al., 2006).

Although salmonid food products are characterized by moderate amounts of lipid contributing to their unique and valued taste, excessive lipid deposition is detrimental for fillet quality. Greater body lipid percentage also increases the amount of slaughter waste (Austreng and Krogdahl, 1987; Kause et al., 2007a). Yet, some products (e.g., smoked fish) may require greater lipid percentage than others. For instance, increasing lipid increases the overall consumer preference of smoked products (Robb, 2002).

In the current data, increased fillet lipid% was phenotypically and genetically related to increasing condition factor (i.e., to unfavorable round body shape). This can be used for the benefit of breeders because selection for slender body shape is easy to implement (Kause et al., 2003, 2004) and in European whitefish it seems to reduce lipid deposition. However, in rainbow trout, condition factor and lipid traits are weakly genetically correlated (Kause et al., 2002). Condition factor alone is an unstable indicator trait for either lipid deposition or fillet yield. This is because both extensive muscle growth (desired characteristic) and extensive visceral lipid deposition or internal organ growth increase condition factor, making condition factor a composite trait. Our results proved further that the Distell Fish Fat Meter was a reliable indicator for fillet lipid% recorded from live individuals, and should be useful in the selection program. The Distell meter gave repeatable readings for fillet lipid content, and moderate accuracy was achieved with 4 measurements per fish. Previous studies have shown that the Distell meter can be used as tool to select for reduced fillet lipid (Quillet et al., 2005) and to produce logical genetic relationships with production traits (Powell et al., 2008).

Fillet Lightness

The color of fresh European whitefish fillet is light gray, and during cooking the color turns to white. Fillet lightness is the most important color trait for European whitefish, with breeders aiming to have light fillet color. In contrast to the red-fleshed salmonids, color additives are not used in European whitefish feeds. Feeds with red color additives constitute a large proportion of total feed costs in red-fleshed salmonids (Alfnes et al., 2006). Thus, the interest toward improving pigment retention and fillet color are less in European whitefish than for red-fleshed Atlantic salmon and rainbow trout (Gjerde and Schaeffer, 1989; Gjedrem, 1997; Kause et al., 2002, 2008; Neira et al., 2004; Quinton et al., 2005; Powell et al., 2008).

The current study showed modest selection potential for fillet color. Heritability of fillet lightness was 0.16. In rainbow trout, CIELAB fillet color traits (lightness, chroma, and hue) have greater heritabilities (0.32 to 0.46), whereas the heritabilities for fillet color visually scored using the Roche color fan are less (Gjerde and Schaeffer, 1989; Gjedrem, 1997; Kause et al., 2002, 2008; Neira et al., 2004; Quinton et al., 2005; Powell et al., 2008).

For European whitefish, breeders want to avoid extensive lipid deposition and to maintain light fillet color. Thus the observed significant positive genetic correlation of fillet lipid% with fillet lightness is unfavorable. This relation may occur because increasing lipid between the myomeres contributes to lighter fillet color. In red-fleshed salmonids, the same genetic relationship

is favorable because dark red, not whitish, color is preferred (Kause et al., 2008).

Relation of Quality with BW

According to Johnston et al. (2007), industry and scientific discussion often assume that increased growth rate, due to intensified management, high energy feeds, or selective breeding, may lead to impaired fillet quality traits including soft texture and increased gaping. In salmonids, it is well known that sole selection for rapid growth increases lipid deposition as a correlated genetic change (reviewed by Gjedrem, 1997; Kause et al., 2007c). Apart from lipid deposition, there were no other unfavorable genetic relationships between harvest weight and fillet quality in European whitefish. Accordingly, the presumption made that selective breeding would reduce fillet quality other than lipid content was not supported by our data.

Harvest weight was favorably genetically related to fillet lightness, rapid growth being related to lighter white color. This may be because the fish with increased harvest weight had greater fillet lipid%. In red-fleshed salmonids, preferred dark red color is mainly favorably genetically correlated with rapid growth (Gjedrem, 1997; Kause et al., 2002; Quinton et al., 2005; Powell et al., 2008).

However, at the phenotypic level, several disadvantageous relationships between harvest weight and fillet quality were observed. Increasing harvest weight was unfavorably related to increased gaping and decreased texture (soft muscle). In contrast to our study, Neira et al. (2004) estimated phenotypic and genetic correlations between harvest weight and fillet texture to be weak or favorable ($r_P = -0.01$ to 0.22 ; $r_G = 0.30$ to 0.70). Johnston et al. (2007), in turn, found thermal growth coefficient (TGC) to display a nonsignificant, significantly positive, or significantly negative correlation with flesh firmness (shear test). Neither Kiessling et al. (2004) nor Johnston et al. (2007) found a relationship between gaping and TGC, growth rate, or harvest weight. Thus, results have been very variable even within a single study. It remains important to understand the underlying methodological or biological causes (or both) of this variability.

In the current data, greater harvest weight was strongly phenotypically and genetically related to greater fillet lipid% and to greater condition factor, as expected (Gjedrem, 1997; Kause et al., 2007c). Likewise, carcass% was negatively and unfavorably phenotypically and genetically related to harvest weight, implying that increased harvest weight was related to reduced carcass%, and thus to increased viscera%. In rainbow trout, viscera% is an indicator trait of visceral lipid (Tobin et al., 2006; Kause et al., 2007a). Therefore, it is possible that increased harvest weight is related to increased visceral lipid in European whitefish too.

This result is of concern for a breeding program. Selection for increased harvest weight will increase lipid deposition and viscera%, but not fillet percentage at a given age. One solution to reduce this problem is to select for gutted weight instead of intact harvest weight. This is beneficial because gutted weight displays more favorable correlation structure with yield traits both in European whitefish (the present study) and rainbow trout (Kause et al., 2007a). This is logical because intact harvest weight is influenced by visceral lipid and viscera%, which reduce yields. Moreover, when selecting for rapid growth, lipid percentage must be selected against, even if only to maintain a stable amount. Because lipid deposits at different body locations are genetically different traits (e.g., fillet and visceral lipid), several lipid traits should be selected simultaneously (Gjerde and Schaeffer, 1989; Kause et al., 2002, 2007c, 2008; Tobin et al., 2006).

Rye and Gjerde (1996) stressed that selection for faster growth is expected to reduce age at slaughter in future generations. If fish are slaughtered at a fixed average weight rather than at a fixed age, the disadvantageous effect of increased growth on lipid percentage may be reduced. However, in Finland, the timing of slaughter also depends on prevailing market prices, which display a seasonal trend. Farmers adjust slaughter time to fit periods of high market prices. Thus, fish are not always slaughtered at a fixed BW.

Genetic correlations between harvest weight and fillet weight are typically highly positive in fish. Thus, selection for increased harvest weight increases fillet weight as a correlated genetic change (Nguyen et al., 2010). This is beneficial because fillet weight is economically the most valuable part, and it can be indirectly selected via easily recorded harvest weight. Compared with fillet weight, fillet% has less positive or close-to-zero genetic correlations with harvest weight (Kause et al., 2002, 2007a; Rutten et al., 2005; Nguyen et al., 2010; this study), and fillet percentage improvement via growth selection may be difficult (Kause et al., 2007a; Nguyen et al., 2010). Fillet percentage is challenging to record without killing animals, and filleting is costly. Thus, methods to predict fillet weight and fillet percentage from more easily measured slaughter traits such as visceral percentage or from body dimensions of live fish have been tested (Rutten et al., 2004; Kause et al., 2007a; Nguyen et al., 2010). Moreover, in some species fillet weight and fillet percentage are positively genetically correlated (Nguyen et al., 2010), and thus selection on the predicted fillet weight may also improve fillet percentage. Yet, in our study the genetic correlation between fillet weight and fillet percentage was only marginally significant (0.42 ± 0.22). Moreover, fish tend to maintain fillet weight proportional to BW, which reduces genetic and phenotypic variance in fillet percentage, reducing the selection potential of this trait (Weatherley and Gill, 1983; Shearer, 1994; Rutten

et al., 2004; Kause et al., 2007a; Powell et al., 2008; Nguyen et al., 2010).

Relation of Quality with Carcass and Fillet Percentage

Both carcass and fillet percentage are traits of great economic interest because they affect production efficiency of a fish supply chain. Fish farmers typically sell whitefish as gutted, with increased carcass percentage being beneficial for farmers. Fillet percentage is expressed at processing, and thus processors in particular benefit from improved fillet percentage. The results provided no evidence that these 2 production traits would be unfavorably genetically related to the quality traits. All genetic correlations of fillet% and carcass% with the quality traits were low and nonsignificant. This again emphasizes that the production traits were weakly genetically related to quality.

In red-fleshed salmonids, estimated genetic correlations of carcass% and fillet% with fillet color score have been low (-0.00 and 0.05 : Kause et al., 2002), and genetic correlation of carcass% with color score negative but nonsignificant (-0.39 : Rye and Gjerde, 1996; -0.45 : Gjerde and Schaeffer, 1989). For carcass% and fillet%, significant or marginally significant unfavorable genetic correlations with fillet lipid% have been found for rainbow trout (0.38 and 0.34 : Kause et al., 2002) and between fillet lipid% and carcass% in Atlantic salmon (0.59 : Rye and Gjerde, 1996). Gjerde and Schaeffer (1989) found correlations of 0.24 between carcass% and flesh lipid% in rainbow trout. This indicates that in contrast to European whitefish, carcass%, and fillet% may be unfavorably genetically related to lipid deposition in red-fleshed salmonids.

At the phenotypic level, decreased carcass% (and thus increased viscera%) was related to increased fillet lipid% and greater condition factor, the correlation structure of viscera% thus being typical for a lipid trait. This may reflect the fact that carcass% is the reverse of viscera%. And at least in rainbow trout, viscera% can be regarded as a lipid trait reflecting visceral lipid (Tobin et al., 2006; Kause et al., 2007a).

At the phenotypic level, greater fillet% was unfavorably related to many quality traits. Greater fillet% was unfavorably related to decreased texture (softer fillet), greater fillet lipid%, decreased fillet lightness (darker fillet), and greater condition factor (round shape), but phenotypically favorably related to greater fillet protein%. Similar phenotypic correlations were observed for BW. This result again indicates that the traits are related to each other at phenotypic but not at genetic level.

Relation of Quality with Maturity Score and Survival

Maturity score had marginally significant negative genetic correlation with fillet lipid%, showing that early

maturing fish had less fillet lipid%. Maturity score had strong negative phenotypic and genetic correlations with carcass%, and therefore decreased carcass% was associated with early age of maturation. These results are logical because mature fish had initiated gonad development, which decreases their carcass% (i.e., increases their viscera%) and fillet lipid% (Aksnes et al., 1986). All other genetic correlations of maturity score with the quality traits were low or with large SE. Maturity score had positive phenotypic correlations with fillet lightness and texture. Therefore, mature fish tended to have fillets with lighter color and firmer texture. The respective genetic correlations were low.

European whitefish is a novel farmed species. Survival was unusually poor (25%) and vertebrae defects observed on filleted fish were unusually frequent (52.7%) in the current study compared with well-established species such as rainbow trout. The values here are greater than normally observed for rainbow trout both with respect to survival (mean survival = 71%, range 54 to 88%, $n = 21$ -yr class-environment combinations) and externally visible vertebrae defects (mean = 6.9%, range 2 to 24%, $n = 7$ -yr class-environment combinations; Kause et al., 2007b; Vehviläinen et al., 2008). The exact cause of these rates could not be established. No disease outbreaks were observed, and feed was confirmed to have appropriate composition, but hard winter conditions with temporal water supercooling occurred, which provides a potential explanation. European whitefish is more sensitive to abnormal management conditions than rainbow trout (S. Airaksinen, personal observations). Vertebrae defects and increased mortality are common among novel farmed species. For example, Dupont-Nivet et al. (2008) and Kolstad et al. (2006), estimating genetic parameters for growth and maturity age at harvest size, found vertebrae defect incidences of 55 to 83% for sea bass (*Dicentrarchus labrax* L.) and 25 to 74% for cod (*Gadus morhua* L.), respectively. Moreover, because mortality can be caused by many different unidentified factors whose incidence varies in time and space, the results presented here for survival may be specific to this particular cohort (Vehviläinen et al., 2008, 2010).

Survival heritability was moderate at 0.19 on the liability scale. This is partly at odds with the common assumption and observation that because survival is a fundamental component of fitness, it should display very low heritability (Fisher, 1930; Mousseau and Roff, 1987; Vehviläinen et al., 2008). However, within discrete cohorts experiencing homogenous environmental conditions and thus potentially the same mortality factors (e.g., a single generation reared in a common environment), survival can display very high genetic variation (h^2 up to 0.71; Vehviläinen et al., 2008). For survival of cod, Atlantic salmon, rainbow trout, and Nile Tilapia (*Oreochromis niloticus*), heritabilities between 0.0 to 0.14 have been estimated (Rye et al., 1990; Gjerde et al., 2004; Charo-Karisa et al., 2006).

To our knowledge, there are no previous estimates of genetic correlations of survival with quality traits in farmed fish. Survival had generally low genetic correlations with all quality traits. If any trend is visible, then increasing fillet lipid% may be genetically related to increased survival. This may be, however, a side effect of the large fish with greater lipid% surviving slightly (but nonsignificantly) better than the small fish with reduced fillet lipid%.

Similarly, genetic correlations of survival with the production traits were low. Because survival is a binary trait, differences in breeding values between surviving individuals are determined only by the survival information of their relatives. Accordingly, it would be useful to find continuously distributed traits that are genetically correlated with survival. These traits would provide additional information on the genetic potential of individuals to survive, increasing the accuracy of estimated breeding values for survival. In the current data, BW and fillet lipid% were the most promising traits for this purpose, but only with weak to moderate positive correlations.

Conclusions

Here we have provided a genetic basis for assessing the potential to improve product quality via selective breeding. All traits except fillet gaping and fillet protein% showed significant genetic variation to be exploited by selection. In general, there was no evidence that genetic increase in growth rate would lead to a reduction in fillet quality traits other than fillet lipid%. There was no evidence that increasing fillet lipid% is genetically related to degradation in other fillet quality traits. Many phenotypic correlations between the production and quality traits were unfavorable and the respective genetic correlations were the same sign but nonsignificant, implying that weak-to-moderate unfavorable genetic relationships may exist, but we were unable to verify them statistically. Maintaining appropriate product quality is fundamental for the success of the whole food supply chain.

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