Norwegian University of Life Sciences
Faculty of Biosciences
Animal and aquacultural sciences

Philosophiae Doctor (PhD)
Thesis 2021:39

Quantitative genetics of growth rate and carcass quality traits in Atlantic salmon

Kvantitative genetiske parametere for kvalitetsegenskaper og tilvekst hos Atlantisk laks

Ólafur Hjörtur Kristjánsson

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1 Abbreviations and definitions

BW	Body weight
CPLS	Canonical partial least squares
EBV	Estimated Breeding value
FCR	Feed conversion ratio
FF	Fillet fat
FP	Fillet pigmentation
GR	Growth rate
MAS	Marker-assisted selection
NIR	Near-Infrared Spectra
Pit-tag	Passive integrated transponder tag
PLS	Partial least squares
QTL	Quantitative trait loci
RAS	Recirculating aquaculture system
RF-ID	Radiofrequency identification tag
RMSEP	Root mean square error or prediction
SA	Standard age, trait measured at a similar age
SW	Standard weight, trait measured at similar BW
TBV	True breeding value
TGC	Thermal growth coefficient
VF	Visceral fat index
VIS	Visible Infrared Spectra

2 List of papers

1. Kristjánsson, Ó. H., Gjerde, B., Ødegård, J., and Lillehammer, M. (2020). Quantitative Genetics of Growth Rate and Filet Quality Traits in Atlantic Salmon Inferred from a Longitudinal Bayesian Model for the Left-Censored Gaussian Trait Growth Rate. *Front. Genet.* 11, 1494. doi:10.3389/fgene.2020.573265.

2. Kristjánsson, Ó. H., Gjerde, B, Lillehammer, M. (2021). Stochastic simulation to evaluate the sensitivity of (co)variance estimates from a longitudinal Bayesian model for the left-censored Gaussian trait growth rate and the correlated trait fillet fat in Atlantic salmon (in manuscript).

3. Kristjánsson, Ó. H., Gjerde, B., Lillehammer, M. (2021). On adjustment of fillet fat for body weight when the traits are recorded on Atlantic salmon at the same age. (in manuscript).

3 Abstract

Quantitative genetic parameters of quality traits and growth rate in Atlantic salmon are commonly recorded at a target average market body weight (4-5 kg) at which the individuals are at the same age, which is less labour demanding than recording the quality traits through repeat slaughtering of fish at same body weight, especially for fish reared in net-cages in the sea. Published estimates of genetic parameters for quality traits recorded on fish of the same age indicate a relatively high positive genetic correlation between growth rate and fillet fat and negative correlation between growth rate and visceral fat as well as between growth rate and fillet pigment. Since the most likely breeding goal for quality traits is their value at the same body weight and the quality traits should ideally be recorded on fish at the same body weight.

The first paper aimed to estimate a reliable genetic parameter for growth rate, fillet fat, fillet pigment, and visceral fat (index) based on traits recorded on fish of about the same body weight. That was possible since the fish population were reared in tanks onshore, which allowed slaughter and recording of only the largest fish at several repeated and following slaughter events. For comparison, another group of individuals from the same families were slaughtered and recorded at the same age. The recorded data were analysed with a Bayesian statistical model. The model aims to account for selecting only the largest fish at each slaughter event. The model uses Gibbs sampler, which assigning a most likely growth rate record to the non-slaughtered and non-recorded fish at each slaughter event. For the fish recorded at about the same body weight, the genetic correlations between growth rate and the three other traits were very different from those obtained based on data recorded at the same age; and the latter estimates were similar to published estimates.

In the second paper, the main objective was to investigate to what extend the Bayesian model in the first paper managed to account for the mentioned selection in the data and thus produce unbiased genetic parameters analysed using stochastic simulation. Additionally, were investigated the effect on the estimated parameters of performing a different number of slaughter events and different increase in fillet fat with increasing age or body weight of the fish. It was concluded that the Bayes model did manage to correct for selection in the trait growth rate, at least for a

population of 2000 animals. For 2000 individuals was found that he appropriate number of slaughter events was six or more, to obtain unbiased parameter estimates. Since the accuracy and genetic correlation did not change much by performing more samplings than six. Then the magnitude of the genetic correlation between growth rate and fillet fat become more different from the genetic correlation between fillet fat an growth rate obtained at same aged individuals and the difference increased, the more the fillet fat increases with the age or body weight of the fish.

In the third paper, the aim was to study how to obtain genetic parameters and breeding values for traits recorded on fish slaughtered at the same age comparable to those obtained when slaughtering the fish at the same body weight. It was found that if the breeding goal is to reduce fillet fat and increase growth rate, adjusting fillet fat for body weight gives a higher genetic gain in growth rate and a minor reduction in fillet fat than performing no adjustment of the fillet fat records. However, if the breeding goal is to increase both traits, no adjustment of fillet fat for body weight should be performed. That was also the conclusions when applying the same adjustment methods on the real data set from the first paper.

4 Norsk sammendrag

Kvantitative genetiske parametere for kvalitetsegenskaper og tilvekst hos Atlantisk laks blir ofte estimert basert på registreringer i en referansepopulasjon ved en ønsket gjennomsnittlig kroppsvekt (4-5 kg), og på et tidspunkt der alle individene er av samme alder noe som er mye mindre arbeidskrevende enn om en skulle gjøre dette ved plukkslakting ved omtrent samme vekt, spesielt ved oppdrettet i en merd i sjøen. Tidligere estimater av genetiske parametere for kvalitetsegenskaper registret på individer av samme alder indikerer en relativt høy positiv genetisk korrelasjon mellom tilvekst og filetfett og innvolls fett og negativ korrelasjon mellom tilvekst og fillet farge. Siden det mest sannsynlige avlsmålet for kvalitetsegenskaper er deres verdi ved samme vekt på fisken, bør også kvalitetsegenskapene ideelt sett måles på individer av samme størrelse.

I den første artikkelen var målet å estimere pålitelige genetiske parameter for tilvekst, fillet fett, filetfarge og innvollsfett (indeks) basert på data registrert på individer med omtrent samme kroppsvekt. Dette var mulig siden fiskene ble oppdrettet i kar på land, noe som gjorde det mulig å slakte og registrere bare de største fiskene på flere etterfølgende tidspunkt og på denne måten oppnå omtrent samme størrelse på fiskene ved registrering av de undersøkte egenskapen, og også under et mye mer konstant oppdrettsmiljø enn mulig i en merd i sjøen. Til sammenligning ble en annen gruppe individer fra de samme familiene slaktet og registrert ved samme alder. De registrerte data ble analysert ved hjelp av en bayesiansk statistisk modell som korrigerer for at bare de største fiskene ble slaktet ved hvert tidspunkt noe som gjøres ved å estimere og tildele en mest sannsynlig vekt til hver av de ikke slaktede og ikke registrerte fiskene på hvert tidspunkt. For fiskene registrert ved omtrent samme vekt ble den genetiske korrelasjonen mellom tilvekst (g/dag) og de tre andre egenskapene funnet å være svært forskjellige fra de basert på data registrert ved samme alder; og de sistnevnte estimatene var i samsvar med tidligere publiserte estimater.

I den andre artikkelen var målet å evaluere i hvilken grad Bayes-modellen brukt i den første artikkelen klarte å korrigere for den nevnte seleksjon i data og produsere forventnings rette parameterestimater; noe som ble undersøkt ved hjelp av stokastisk simulering. I tillegg undersøkte vi effekten på de estimerte parameterne

både av ulikt antall slaktetidspunkter og av ulik økning i filetfett med alder eller vekt på fisken. Det ble konkludert med at for en populasjon på 2000 fisk er det optimale antall slaktetidspunkt seks eller flere, siden alle scenarier med minst seks slaktinger ga tilnærmet lik genetisk korrelasjon mellom egenskaper og sikkerhet på avlsverdier. Den genetiske korrelasjonen mellom tilvekst og filetfett estimerte basert på data registrert ved samme vekt blir mer forskjellig fra den registrert ved samme alder jo mer filetfett øker med alder/vekten på fisken

I den tredje artikkelen var målet å undersøke hvordan man kan oppnå genetiske parametere og avlsverdier for egenskaper registrert på fisk slaktet ved samme alder som er sammenlignbare med de som blir estimert ved samme kroppsvekt, Dette ble også undersøkt ved hjelp av stokastisk simulering og ved å korrigere filet fett på fire ulike måter; pre-korrigere ved hjelp av regresjonen av filetfett på vekta av fisken, inkludere vekt som en kovariabel i den statiske modellen for filet fett, pre-korrigere ved hjelp av regresjonen av filet feitt på residualen av vekta på fisken, eller inkludere residualen av vekta på fisken som en kovariabel i den statistiske modellen for filet fett. Det ble funnet at hvis avlsmålet er å redusere filetfett og øke tilveksten, vil korrigering av filetfett for kroppsvekt (ved hjelp av pre- eller kovariabel) gi høyere genetisk framgang for tilvekst og en mindre reduksjon i filetfett sammenlignet med ingen korrigering av filetfett. Imidlertid, hvis avlsmålet er å øke begge egenskapene, bør filetfett ikke korrigeres for kroppsvekt. Dette var også konklusjonene når samme type korrigeringer av filetfett for kroppsvekt ble brukt på datasettet fra første artikkel, hvor fisken ble slaktet ved samme alder.

5 Synopsis

5.1 Introduction

5.1.1 Background

The first selective breeding program for Atlantic salmon was established in Norway by AKVAFORSK (now Nofima) in the early 1970s based on wild salmon collected from several rivers in Norway (Gjedrem, 2010). Several breeding programs have been established from 1980 and onwards using that material, both within Norway and in other countries. Example of countries that have received the Norwegian material and carried out breeding are the UK, Faroe Islands, Ireland, Chile, and Iceland, where the material was used to establish separate breeding programs or crossed with domestic Atlantic salmon strains (Fao, 2021; Janssen et al., 2015).

Most of the breeding programs are in their 11-14 generation of selection with a generation interval of 3-4 years. Published estimates of genetic gains for traits selected for or correlated responses in other traits are few. Most of the publications are comparing growth or quality traits between wild and farmed salmon. Growth rate after five generations of selection compared to wild salmon showed 113 % increased growth rate and 20 % reduction in the feed conversion ratio (kg feed consumed per kg growth, FCR) (Thodesen et al., 1999). More recent studies have shown that farmed fish grow 2.9 times faster than wild fish (Solberg et al., 2012). Comparison of fillet fat between wild and farmed revelled minimal difference (12.58 % farmed, 11.72 % wild) in fillet fat, but large and significant difference in pigment (6.01 mg/kg farmed, 3.18 mg/kg wild) (Solberg et al., 2012)while other study revealed higher fat content and pigment in farmed salmon (8.43 mg/kg vs 6.44 mg/kg and 12.5 % vs 6.8 % lipid) compared to the wild (Johnston et al., 2006).

The Atlantic salmon breeding programs apply a combination of family and within-family selection where the pedigree of all tested animals and breeding candidates is available by either identifying the animals by using passive integrated transponder tags (PIT-tags) after a period of separate rearing of the families or by pit-tagging and genotyping a tissue sample of the animal and their parents which allows for pooling a sample of the eyed eggs or fries from each family at an early stage.

In recent years, the Atlantic salmon breeding programs have implemented genomic selection (GS) (Meuwissen et al., 2001) based on a set of single nucleotide polymorphism (SNP) determined by genotyping, which increases both selection intensity and accuracy and thus the genetic gain, in particular for the traits in the programs (specific disease traits, carcass quality traits) than cannot be recorded on the live breeding candidates(Sonesson and Ødegård, 2016). The genotypes can also identify quantitative trait loci (QTL) to perform marker-assisted selection (MAS). (Jansen and Stam, 1994; Rye et al., 2010).

The breeding goal of growth rate is to reduce the number of days to market weight (4-5 kg). The body weight records (from which growth rate is calculated) are obtained on a population of breeding candidates and a population of their sibs; both preferably reared in a commercial farm environment. When the mean body weight of the fish has reached the desired average market weight, all animals are slaughtered and measured at the same age. At the same time, additional traits are recorded, i.e., fillet fat (%), fillet pigment (mg/kg), visceral (fat) weight or index (visceral weight/body weight). Due to the selection practised for increased growth rate, the recording of body weight occurs at a younger age in each new generation.

A premium is paid for larger fish (7-8 kg) (NASDAQ, n.d.). Documentation of why a premium is paid for larger salmon does not exist by author knowledge. Probable explanations why less volume of large fish is slaughtered at 7-8 kg body weight compared to slaughtering at 4-5 kg body weight can be the biological limits are met at 4-5 kg mean body weight of the sites, or farmers do want to have the fish for as short period as possible to decrease the risk of a disease outbreak. Another reason for a premium price for 7-8 kg fish could be higher fat levels in the fillet. In a survey where salmon were sampled across Norway at an average body weight of 5.2 kg was found that fillet fat was 16.5 % which can thus be considered the average fillet fat in the industry in Norway (Aas et al., 2019), so fish at 7-8 kg have maybe 20 % fillet fat which could be considered as the fillet fat threshold for raw consumption. The consumption of raw salmon will probably increase since the predicted increase of Sushi was estimated at 5.34 % from 2018-2022 (Research and markets, 2018) and among popular Sushi meals is raw salmon. Given the above, a possible breeding goal for fillet fat could be to increase fillet fat so that the desired fillet fat level is achieved for a smaller sized (4-5 kg) fish, but probably at the cost of a higher FCR as evidence has shown that reducing fillet fat can potentially lower FCR (Kause et al., 2016). Improving FCR is of high importance since feed cost is estimated to be half of the

production cost (Fiskeridir, 2019). Fish with a higher fat level than other fish in the population should, by theory, need more energy to maintain the energy status as they grow. Theoretical calculations have shown that a 1 %-unit reduced body fat will reduce the energy needed by 0.4 MJ/kg, which corresponds to a 0.034 reduction in FCR (T. Åsgård pers. comm). For the Norwegian industry, which in 2020 produced 1.4 billion tons of Atlantic salmon, this corresponds to about 50.000 tons of feed saved.

Excess visceral fat is a waste product, and the breeding goal for this trait is, therefore, to reduce it to a level where it does not have a negative effect on the breeding animal's fitness and reproduction ability since visceral fat is mobilised during sexual maturation (Aksnes et al., 1986). Reducing visceral fat probably improves the FCR. Visceral fat records can be obtained by directly measuring the amount of fat in the visceral, which is very laborious, or by recording the weight of the visceral and express it relative to the body weight of the fish (visceral index). The variation in the visceral index is most likely due to variation in visceral fat since intestines make up a stable proportion of the visceral (Rye and Gjerde, 1996).

The breeding goal of pigmentation is to increase the animals' retention ability to the pigment additives in the feed. The proportion of fish oil has been reduced and replaced by soybean oil in recent years (Aas et al., 2019). Some evidence shows that increased soybean oil reduces the ability of the fish to retain the pigmentation from the feed (Bævre-Jensen, 2020). Consumer studies have also shown that consumers are more willing to buy dark coloured salmon fillets (Alfnes et al., 2006; Steine et al., 2005), therefore is the selection for increased pigmentation retention among the essential traits in current breeding programs. The cost of pigment in feed has been reduced substantially and accounts only for 1.1-3.6% of the feed cost (Cargill) as compared to 15%, 15 years ago (Alfnes et al., 2006; Steine et al., 2005), so the aim with the breeding objective of fillet pigment has changed from increasing the retention to give the possibility to reduce the amount of pigment additive in the feed to reduce the feed cost into improving the animals ability to retain sufficient amounts of pigment additives when the fish is feed of more soybean oil-based feed.

In addition, comes several diseases (e.g., IPN, PD, CMS, HSMI) and parasites (e.g., lice, AGD) causing mortalities or high treatment costs. For some diseases (e.g., ISA), the entire population at the rearing site must be eliminated. Therefore, a disease outbreak may have a large negative impact on production. The breeding companies

apply various selection strategies to increase resistance and/or tolerance to the pathogens. These traits are obtained by recording the mortality and volume of parasite or a viral load of a sib group of the breeding candidates in a specially designed challenge test for each pathogen.

Land-based salmon farming is a growing sector. Possible reasons for increasing land-based farming can be a high cost of sea cage licences or a limited increase in the number of sea cage licenses issued because of an increasing sea lice problem due to the development of resistance of the lice to available chemicals for delousing treatments. Also, air freight pollution is considered a major contributor to climate change; thus, countries that consume large portions of the salmon produced have established land-based farms ("Massive land-based salmon farm rising in Homestead | Miami Herald," n.d.) and improvements in the recirculating aquaculture systems (RAS) allows for land-based farms where a limited amount of water is available, or water that has previously was too cold for farming can now be used. Since the warming energy is retained in the farm by reusing the warm water. Quality traits are most likely in addition to growth rate more important traits than diseases in land-based farming as diseases have not shown to be of the same magnitude as in sea cage farming, while carcass quality traits and sexual maturation may become more important.

Among the Atlantic salmon breeding companies is a strong competition to increase their market of eyed eggs. All smolt producer in the world can, to a large degree, buy eyed eggs from all breeding companies depending on the regulation in the country the smolt producers are located in and the availability of eggs when they are needed. Therefore, one of the largest challenges for a breeding company is to define which trait should be included and selected for in the breeding objective and the relative economic weights to be given to each of the traits.

5.1.2 Status of knowledge

Previous studies on quality traits in Atlantic salmon have reported relatively high positive genetic correlation (from 0.34 to 0.84) between fillet fat and growth rate while it has been found high negative between visceral fat and growth rate (-0.67) and between growth rate and fillet pigment negative (-0.41) to moderate positive (0.31) (Powell et al., 2008; Rye and Gjerde, 1996; Tsai et al., 2015; Vieira et al., 2007). These parameters are obtained in a group of individuals measured at the same age and thus for individuals an average body weight and therefore of various

body sizes. The most likely breeding objective of quality traits is to improve their trait values at the same body weight, for which no estimate of genetic parameters has been obtained in previous studies. When selection for increased growth rate and reduced or stable fillet fat in a population using current genetic parameters where the individuals are measured at the same age, the high genetic correlation between fillet fat and growth rate gives a problem in selecting animals. A large portion of the selection intensity has to be used to counter-effect the increase in fillet fat when increasing the growth rate. The correlation between body weight and fillet fat reduces if body weight is used as a covariate on fillet fat to reduce the impact of varying body size. When this correlation is reduced, less is used of the index in vain, and more of the selection intensity can be used on selection for growth rate and other traits.

If fillet fat is pre-corrected for the correlated trait body weight of the fish by the regression coefficient of fillet fat on body weight, or by including body weight as a covariate in the statistical model for fillet fat, the genetic variation in fillet fat is reduced, which result in a less genetic gain in fillet fat. The same principle applies to other quality traits such as pigment and visceral fat since a genetic correlation between growth rate and visceral fat has been found.

Since the growth rate has improved in salmon breeding programs (Glover et al., 2017), the recording of the traits occurs at a younger age. Since the recording occurs at a younger age, the recordings are likely to occur in a different season than the recording in the previous year class. Seasonal changes in deposition of filet fat increases during declining day length in autumn (Rørvik et al., 2018). It has also been shown that the genetic correlation within the trait growth rate between time points is not unity (Gjerde et al., 1994); therefore is it essential to estimate the genetic parameters at a certain body weight instead of a certain age; thus, the records over time are obtained at a younger age due to the improved growth rate. Other quality traits such as pigmentation and visceral index are also correlated to growth rate/body weight and are for the same reasons probably not obtained at an optimal time point when recorded at the same-aged population. Therefore, are the phenotypes for the quality traits obtain currently for quantitative genetic parameter estimation, not in line with the trait definition.

5.2 Objectives

In this study, the most likely breeding objective for carcass quality traits in Atlantic salmon was defined as their trait values recorded at a desired marketing body weight (e.g., 4-5 kg) of the animals. The main aim was to develop and evaluate possible methods to improve the quality traits, as they are defined in the breeding objective, i.e., at market weight. To obtain such trait records directly is very laborious as this would require repeat grading and handling and thus imposed stress on the fish with the risk for both reduced growth and increased mortality, particularly for fish reared in a net-cage in the sea. Therefore, more practical methods were tested in this study, including sample slaughter of batches of fish with approximately the same weight and statistical methods to correct for the sampling or to adjust records to a given weight.

This was obtained through the following three sub-goals:

- Reveal the sensitivity of trait parameters for time of measure through obtaining reliable genetic parameter estimates for growth rate, fillet fat, fillet colour and visceral fat when the traits are recorded on fish of the same age as well as of about the same body weight.
- Investigate through stochastic simulation if the genetic parameters obtained from the fish slaughtered at about the same body weight in the real data set are unbiased, and to what degree the parameters are affected by the number of slaughter events and by how fast fillet fat are being deposited by the age or body weight of the fish.
- Investigate through stochastic simulation how to correct breeding values for traits recorded on animals of the same age to increase their ability to predict the traits at the same body weight.

5.3 Material and methods

The data in this thesis is based on traits recorded on two groups of Atlantic salmon, one slaughtered and recorded at the same age (SA) and one (sibs of the first-mentioned population) slaughtered and recorded at about the same body weight (SW). The (co)variances obtained from these data set were used in a stochastic simulation to investigate to what degree the Bayesian model used to analyse the SW data managed to produce unbiased (co)variance, also under different experimental design than was used for the real data.

5.3.1 Real data set

The Atlantic salmon in the real data set originates from the breeding company Stofnfiskur (www.stofnfiskur.is) located in Iceland. Stofnfiskur rears all salmon on land in tanks using borehole seawater in two salmon farms Vogavík and Kalmanstjörn, located in the Reykjanes peninsula.

Figure 1 Locations mentioned in Paper 1, year class 1 was reared in Kalmanstjörn, and the material in year class 2 was reared in Vogavík. Both year classes were hatched in Kollafjörður hatchery.

Since the fish is reared in tanks on land, it is possible to do repeated recordings at low cost and low handling stress to the animals.

Figure 2 Sorting and sampling of the material in yc 1 at the Kalmanstjörn farm in Iceland. Water lowered in the tank, and sorting grids inserted. Fish anaesthetized and then measured to determine if they are above the set threshold body weight. If they are bellow, they are put back into the tank.

The material used originates from two-year classes. The year classes were produced in fall 2008 (yc 1) and spring 2009 (yc 2) using a nested mating design, where each male was mated to two females in most cases, and each female to one male only. Yc 1 consisted of 106 full-sib families (offspring of 106 females and 68 males), and yc 2 of 100 families (offspring of 100 females and 52 males). At 2.5 kg (2.7 kg yc 2) body weight, the used fish material in this study was randomly selected from a larger population, and the body weight recorded and placed into an experimental tank for each year-class. Within each year class, two experimental groups were made; one that was measured at the same age (SA) and the other that was measured at the same body weight (SW). Rearing of the SA group was until a mean market body weight (4.4 kg yc 1, 4.6 kg yc 2) and then the group was slaughtered, and the traits recorded.

Figure 3 Measuring fillet weight of both fillets of each individual of year class 1 at the Kalmanstjörn farm.

The SW group sampling within each year class was when approximate one-sixth of the largest individuals achieved a mean body weight of 4.6 kg. At first sampling, this was done by sampling all individuals passing 4.2 kg, while for the next four samplings, all individuals passing 4.4 kg were sampled. At the sixth and last sampling, all reaming individuals where sampled. The last sampling was done 29(yc 1) and 34(yc 2) days after the fifth sampling in the year classes. More details about the rearing and sampling are in Paper 1. At each sampling, the PIT-tag, body weight, body length and tank of origin were recorded. The growth rate (GR) of each fish was

calculated by dividing the body weight by the age of the fish. At slaughtering, the fillet weight, sex, visceral weight, fillet fat % (FF) and fillet pigment (FP) as mg/kg pigment additives (Astaxanthin + Canthaxanthin) was recorded. Recording from both fillets was obtained, and their mean reported as the individual value. The fillet fat and fillet pigment were obtained using the machine Qmonitor (Tomra, 2020), which measures fillet fat in the Near-Infrared Spectra (NIR) and fillet pigment in the Visible Light Spectra (VIS) light region by passing the fillets under the machine using a conveyor. The visceral weight record was used to obtain the visceral index (VF) by dividing visceral weight by round body weight.

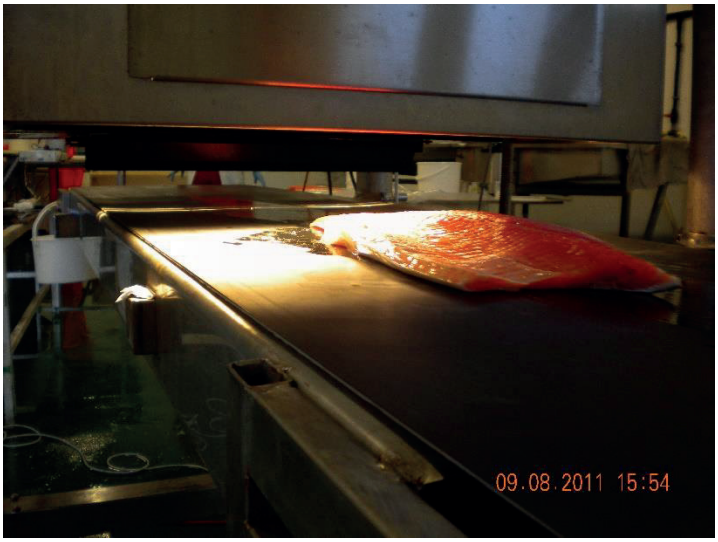

Figure 4 Measuring fillet fat and fillet pigment using the Qmonitor machine.

5.3.2 Stochastic simulation

In paper 2 and 3, a stochastic simulation program was developed, which made it possible to perform simulated repeated slaughtering as performed for the SW group in Paper 1 and with input parameters from the SA group in that paper. The input (co)variance for a single time point (day) were those obtained from the SA group. The phenotypic variation was segmented into additive genetic, repeatability and residual variation as in the SW group in the real data set. Phenotypes for fillet fat and growth rate were simulated for 421 days (60 weeks) to mimic the real data set. The residuals were correlated between the traits within the day but did not correlate between days. The mean growth rate of the simulated population was assumed to follow the Thermal Growth Coefficient (TGC) growth curve, which in

combination with a coefficient of variation (CV) was used to scale the simulated breeding value, permanent environmental value and residual value at each day according to the value obtained from the TGC curve for each day.

The true breeding value (TBV) used to calculate bias and accuracy for growth rate was the generated growth rate value prior to any scaling since the sampling point was adjusted for in the parameter estimation. The TBV for fillet fat was taken from the time point in the simulated dataset when each individual first passed 4.4 kg body weight. A detailed description of the simulation algorithm can be seen in Paper 2.

In Paper 3, the TBV for fillet fat (FF) obtained in Paper 2 was compared to the estimated breeding value using the phenotypes obtained when the entire population was at the same age. Several statistical methods were applied in the parameter estimation or applied on the FF phenotype to determine which method gave the estimated breeding value closest to the TBV and the highest selection differentials of the TBV (simulation study) of EBV (real data) for FF and GR(BW for the simulated data).

5.3.3 Statistical methods

A Bayesian multivariate model for a truncated trait was developed for a binomial trait (Ødegård et al., 2010) implemented in the Gibbs sampling module in DMU (Jensen et al., 2014) was used. The model was also capable of estimate parameters for the Gaussian trait(Kristjánsson et al., 2020). The Bayesian model was used to estimate quantitative parameters for growth rate since the registration of growth rate was over a period of time, and since the target was to measure the largest individuals at each sampling, a selection in body weight was needed to be able to obtain registrations of the quality traits at similarly sized individuals. The model simulates growth rate values for the individuals who are still alive at sampling but not sampled using Gibbs sampler. The model uses the growth rate of the individual with the lowest growth rate value at the sampling as a threshold for the Gibbs sampler. Therefore, individuals sampled in the last sampling receive a simulated record at each sampling where they are not sampled until they receive their observed phenotype at sampling. By applying the Bayesian model is the impact of selection on growth rate reduced, and growth rate record obtained for most of the population at each sampling except in the last samplings when a smaller number of individuals are left. Using the simulated growth rate records that the individuals sampled in the last sampling events received, the Bayesian model manages to estimate the population growth rate for most of the sampling events. In the

parameter estimation, eight traits were fitted: growth rate, fillet fat, visceral index, fillet pigment for the group measured at the same age and the group measured at the same body weight, where the Gibbs sampling was applied on growth rate in the same weight group.

In Paper 2, the phenotypes were generated by stochastic simulation and the parameter estimation simplified by not simulating common environmental effect nor other fixed effects than sampling time point for the trait growth rate since the main focus was on the relation between fillet fat and growth rate and how the various number of samplings and increase of fillet fat by age affected the estimated parameters. Thus, a bivariate model was fitted for the traits growth rate and fillet fat when sampling the population at 1, 2, 4, 6, 8, 10, 20, 30 or continuous (C) sampling event number, i.e., sampling each individual when they first achieve 4.4 kg body weight. The Bayesian model was applied for 30 and less samplings where the Gibbs through the censoring model was used to simulated growth rate record for the individuals still alive at sampling but not measured. Fixed effects included where time point of measure for growth rate and the overall mean for fillet fat. For the continuous sampling, a REML model was fitted with the overall mean on both traits as fixed effects.

In Paper 3, four different methods were investigated for how to adjust fillet fat for the body weight of the fish when the traits were assumed to be recorded on fish of the same age. A bivariate model was fitted for the traits fillet fat and body weight or growth rate in the real dataset. Evaluated was to pre-adjust fillet fat prior to the parameter estimation from the bivariate statistical model or include body weight or growth rate as a covariate in the bivariate model. Additionally, we investigated to pre-adjust fillet fat for residual of body weight or include residual body weight as a covariate in the bivariate model. Both data from the simulation developed in Paper 2, and the real data in Paper 1 was used.

The quality of the models and scenarios defined in paper 2 and 3 were evaluated using an accuracy of selection of each trait and the bias of their estimated breeding values.

5.4 Summary of results

5.4.1 Paper 1

For the fish measured at the same age (SA), the estimated genetic parameters agree well with previously published parameters for Atlantic salmon. Heritability of the studied traits; growth rate (GR), fillet fat (FF), fillet colour (FP) and visceral fat index (VF), in the groups SA and SW were similar, about 0.2 for FF, 0.15 for FP and 0.35 for VF and GR, and the genetic correlation between the same trait in the two groups were high and positive for GR (0.91±0.05) and VF (0.86±0.05), medium for FF (0.45±0.17) and low for FP (0.13±0.27). Within-group, the genetic correlation between GR and FF was highly positive within the SA group (0.59±0.14) but negative in the SW group (-0.45±0.16). The genetic correlation between GR and FP changed from negative (-0.33±0.22) in the SA group to positive in the SW group (0.62±0.16). Therefore, the genetic correlation between GR, FF and FP are sensitive to whether they are measured at SA or SW. The genetic correlations obtained between the growth rate and the quality traits are favourable when the growth rate is increased using parameters from the SW group, which is more in line with the quality trait definition.

5.4.2 Paper 2

It was concluded that the appropriate number of slaughter events was six or more to obtain close to unbiased parameter estimates. Since the accuracy and genetic correlation became stable when for the 2000 fish simulated in this study where a constant rearing environment assumed. The growth rate and fillet fat records obtained from the proposed repeated slaughter event scenario and analysed with the applied Bayesian model can be used to obtain genetic parameters for traits at similar body weight.

5.4.3 Paper 3

It was found that if the breeding goal is to reduce fillet fat and increase growth rate, adjusting fillet fat for body weight give a higher genetic gain in growth rate and a minor reduction in fillet fat as compared to performing no adjustment of the fillet fat records. However, if the breeding goal is to increase both traits, no adjustment of fillet fat for body weight should be performed. This was also the conclusions when applying the same adjustment methods on a real data set.

5.5 Discussion

For carcass traits in Atlantic salmon, the most likely definition is their value at a desired market body weight (e.g., 4-5 kg). The main aim was to develop and evaluate possible methods to improve the quality traits, as they are defined in the breeding objective, i.e., at market weight. That was achieved by revealing the sensitivity of the growth rate and carcass traits by obtaining reliable genetic parameters estimations on fish at the same age as well as of about the same body weight. Further, to evaluate if the genetic parameters obtained in the real dataset are unbiased through a stochastic simulation. And then, to study how the parameters are effect by the number of slaughter events and how various rate of fillet fat deposited by age influence the parameters. And finally, to evaluate methods used to correct breeding values on animals of the same age to increase their ability to predict the traits at the same body weight.

The parameters are the first published estimates for the mentioned traits measured on individuals at about the same body weight to authors knowledge. It was found that the genetic and residual correlation between the traits is sensitive to whether they are measured on same-aged or same sized individuals. The estimated genetic parameters also indicated the reranking of families for the quality traits, whether they are measured at the same age or same body weight. Selection for increased growth rate will result in a favourable correlated response in fillet pigmentation, visceral fat and fillet fat if the aim is to reduce or keep fillet fat stable.

The longitudinal Bayesian model for the Gaussian trait growth rate seemed to account for the directional selection for growth rate in the data (Paper 1), and this was further confirmed in the simulation study (Paper 2), where fixed effect estimates followed the true growth curve for slaughtering events except at the last ~1/3 slaughter events. Thus, the Bayesian model can be used to adjust for selection in growth rate when the growth rate threshold is well defined, and the aim is to sample a similar number of a subgroup of the largest individuals over time to obtain unbiased genetic parameters of correlated traits recorded on similarly sized individuals. The Bayesian model managed to account for the selection of the largest fish when six or more simulated slaughter events were assumed in a population of 2000 animals. Based on the genetic correlation and accuracy, which became quite stable at and above six samplings. The Bayesian threshold model for a longitudinal Gaussian trait may also be used in other farm animal species where there is a need to obtain breeding values for traits correlated to growth rate when recorded a given

body weight. For the Gibbs sampler to simulate values to adjust for the selection, the threshold must be well defined where the truncation is performed. The Bayesian model is developed for left, interval or right censoring on Gaussian or Binomial traits (Kristjánsson et al., 2020; Ødegård et al., 2010). Further studies should be conducted on the quality of the estimates when applying a different censoring than in the present study.

In Paper 2, the impact of various increase of fillet fat by age on the parameter estimates for fillet fat and growth rate was investigated using stochastic simulation when their phenotype of the traits is obtained at about the same body weight. If no increase was in fillet fat by increasing age, the genetic correlation maintained the same between fillet fat and growth rate irrespective of the number of subsampling groups. If fillet fat increased by age, the genetic and residual correlation between growth rate and fillet fat become more different from the correlations obtained from a population where the traits were recorded at the same age. Using the real data parameters, the genetic correlation changed from medium positive when measured at the same age to medium negative when the number of subsampling groups increases.

The development of the genetic parameters for fillet fat over time and the residual and genetic correlation to growth rate over time is unknown. In the simulated data set, the intermediate slope for fillet fat produced estimates of the parameters similar to those obtained in the real data set, but the genetic parameters obtained showed to be sensitive to the degree of increase of fillet fat by age. Therefore, is it unknown if the conclusions drawn from Paper 1 would be the same if the target body weight would have been lower or higher than in the real data.

If the studied quality traits could also be recorded on the breeding candidates, both the accuracy of their estimated breeding values and especially the selection intensity would be increased, thus resulting in a higher genetic gain in each of the trait. Limited publications are available on the technology that measures quality traits on live fish with sufficient accuracy on a large number of fish. To be used in practice, such an instrument must also be robust enough to be used close to a net-cage in the sea, and recordings of the traits also have to be done fast with minimum handling to keep mortality low. Especially if the aim is to measure the trait at similar-sized individuals, multiple grading of the fish with respect to their body weight has to be performed, which is complex when the fish are reared in a sea cage.

The benefit of accurate pigment and fillet fat measures would vanish if potentially good individuals died after the recordings were performed. An example of instruments used in terrestrial animals is a CT scanner, which is hard to fit on a boat and measure a large population of breeding candidates.

The third paper showed that to pre-correct fillet fat by phenotypic body weight or use phenotypic body weight as a covariate in the model for fillet fat in the parameter estimation gives the highest overall true genetic gain in body weight and fillet fat when the aim is to decrease fillet fat. If the aim is to increase fillet fat, no adjustment of fillet fat should be performed. Probably other quality parameters correlated to body weight should also be pre-corrected to reduce the impact of body weight when obtained on fish at the same age. An example of such a trait is fillet pigment, with an estimated genetic correlation close to zero (0.13, Paper 1) between the records obtained at SA and SW.

The idea of pre-or covariate adjusts fillet fat for residual of body weight was to not reduce the genetic variation in fillet fat due to the genetic correlation between fillet fat and body weight. These methods reduced the residual correlation between body weight and fillet fat but did not alter the genetic correlation and produced genetic gains comparable to those obtained when performing no adjustment of the fillet fat records.

The parameter estimates from Paper 1 indicate that if the breeding goal is to increase growth, and marginally decrease fillet fat and marginally increase fillet pigment, it may not be necessary to record or select for the two latter mentioned traits. However, if the aim is to reduce fillet fat more than what is obtained through the correlated response from selection for increased growth rate, the traits have to be recorded, and if recorded on fish at the same age, the fillet fat, and probably also the fillet pigment records, should be adjusted for the body weight of the fish. This can be most efficiently done by including body weight as a covariate in the statistical model for fillet fat and fillet pigment. If the aim is to increase fillet fat and growth rate, no adjustment is needed on fillet fat to maximise the genetic gain of both traits. Whether these traits need to be recorded or not depend on the magnitude of the genetic correlation of growth rate with the other traits and the desired magnitude of the gain for these traits relative to growth rate and other traits selected for.

5.6 Identified gaps for future study.

5.6.1 Implications

- A longitudinal Bayesian model for the truncated Gaussian trait growth rate implemented through a Gibbs sampler procedure can be used to obtain reliable genetic parameters and breeding values for both growth rate, carcass and fillet quality traits when performing six or more following slaughtering and recordings of only the largest fish at each slaughtering (except in the last slaughter where remaining fish is slaughtered).
- When performing simultaneously selection for increased growth rate and reduced fillet fat, pre-or covariate adjustment of the fillet fat for body weight gives higher genetic gain for fillet fat and substantial higher genetic gain for growth rate than practising no adjustment of the fillet fat records.
- When performing selection simultaneously for increased growth rate and increased fillet fat, pre-and covariate adjustment of the fillet fat records for body weight will give higher genetic gain for fillet fat but a substantial lower genetic gain for growth rate. Therefore, in this case, it is to be recommended to perform no adjustment of the fillet fat records as this will give the highest overall genetic gain for the two traits.

5.6.2 Gaps

- The assumption of a genetic correlation of unity and residual correlation of zero between days for each trait, regardless of how close or far away these days are to each other, is simplistic.
- To be able to simulate growth rate and quality traits over time closer to real data requires reliable estimates of their (co)variances that could be obtained if all traits could be repeatedly recorded over time. However, this would require technology to record the quality traits accurately also on live fish without affecting the trait values too much.
- Such real repeated data would also provide ideal data to evaluate the ability of the Bayesian model and the Gibbs sampler to impute growth rate data for the non-recorded fish at each slaughter event.
- The predicted genetic gains in Paper 3 are not realistic, as it is performed for two traits only, while it should have been extended to include all traits in the breeding goal to consider correlations between all traits as well as their economic weights.

5.7 Conclusions

Selecting for increased growth rate only will not increase fillet fat or reduce fillet pigment, as previously publications indicated. Rather a reduction in fillet fat and an increase in fillet pigment is to be expected when the fish are slaughtered at the same average body weight and, therefore, at a younger age.

The Bayesian model has shown to be capable of adjusting for selection in a trait such as growth rate and can be used in other fish species or terrestrial animals where there is a need to correct for selection in growth rate or body weight when the aim is to measure the secondary trait at target body weight or any other specific target which implies selection in growth rate or body weight.

Measuring body size dependant traits on animals at similar body weight instead of similar age has shown to be possible and necessary to obtain reliable parameters for such traits.

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7 Papers

Paper 1

frontiers in Genetics

METHODS
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Quantitative Genetics of Growth Rate and Filet Quality Traits in Atlantic Salmon Inferred From a Longitudinal Bayesian Model for the Left-Censored Gaussian Trait Growth Rate

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In selective breeding programs for Atlantic salmon, test fish are slaughtered at an average body weight where growth rate and carcass traits as filet fat (*FF*), filet pigment (*FP*) and visceral fat index (*FF*) are recorded. The objective of this study was to obtain estimates of genetic correlations between growth rate (GR), and the three carcass quality traits when fish from the same 206 families (offspring of 120 sires and 206 dams from 2 year-classes) were recorded both at the same age (*SA*) and about the same body weight (*SW*). In the *SW* group, the largest fish were slaughtered at five different slaughter events and the remaining fish at the sixth slaughter event over 6 months. Estimates of genetic parameters for the traits were obtained from a Bayesian multivariate model for (potentially) truncated Gaussian traits through a Gibbs sampler procedure in which phantom *GR* values were obtained for the unslaughtered, and thus censored *SW* group fish at each slaughter event. The heritability estimates for the same trait in each group was similar; about 0.2 for *FF*, 0.15 for *FP* and 0.35 for *VF* and *GR*. The genetic correlation between the same traits in the two groups was high for growth rate (0.91 ± 0.05) visceral index (0.86 ± 0.05), medium for filet fat (0.45 ± 0.17) and low for filet pigment (0.13 ± 0.27). Within the two groups, the genetic correlation between growth rate and filet fat changed from positive (0.59 ± 0.14) for the *SA* group to negative (−0.45 ± 0.17) for the *SW* group, while the genetic correlation between growth rate and filet pigment changed from negative (−0.33 ± 0.22) for the *SA* group to positive (0.62 ± 0.16) for the *SW* group. The genetic correlation of growth rate with *FF* and *FP* is sensitive to whether the latter traits are measured at the same age or the same body weight. The results indicate that selection for increased growth rate is not expected to have a detrimental effect on the quality traits if increased growth potential is realized through a reduced production time.

Keywords: Atlantic salmon, growth rate, filet fat, filet pigment, visceral fat, Gibbs sampler, censored

INTRODUCTION

Growth rate (*GR*) is among the most important traits selected for in selective breeding programs for Atlantic salmon. Improved growth rate enables faster turnover in production, and this creates economic benefits in terms of reduced fixed and variable costs per kg fish produced. The increased growth rate is expected to reduce the fraction of the nutrient in the feed consumed that is allocated to maintenance and hence, improving feed efficiency. Improved feed efficiency was detected in a farmed salmon population selected for increased growth rate over five generations when compared to wild salmon (Thodesen et al., 1999). Over generations, genetic improvement of growth rate will result in cohorts of fish reaching the appropriate body weight at a younger age, resulting in shorter production time. Therefore, the growth rate to targeted body weight (GR_{SW}) rather than a targeted age (GR_{SA}) is likely the most appropriate breeding objective trait for growth.

Other important breeding objective traits are filet (carcass) fat (*FF*), visceral fat (*VF*) and filet pigment (*FP*). For FF and VF the breeding goal may be to keep or reduce their trait level since increasing body fat could potentially increase feed conversion ratio (*FCR*)as shown in a study of rainbow trout (Kause et al., 2016). Unfortunately, estimates of the effect of selection for reduced *FF*, *VF* or increased *FP* on feed efficiency, or the correlated effect in feed efficiency through selection for other traits (e.g., growth), is not possible to obtain as feed consumed by fullsib families is not possible to obtain on a sufficiently large number of families at an affordable cost. And currently, no tools or equipment are available to obtain individual feed consumption records of fish reared in a group. Breeding goal of *FP* is to increase redness of the filet since consumers are not as willing to buy a pale salmon filet (Steine et al., 2005).

In current breeding programs for Atlantic salmon, the traits mentioned above *GR*, *FF*, *VF* and *FP* are recorded when the average body weight of the test fish group(s) reach a targeted round body weight similar to typical commercial slaughter weight (e.g., 4–5 kg), at which point all fish are slaughtered over a few days, and therefore approximately at the same age (GR_{SA}, FF_{SA}, FP_{SA}, VF_{SA}), or over a few slaughter events to reduce biomass without any particular grading with respect to body weight. The recording of the traits is therefore not performed at a specific body weight in line with the ideal definition in the breeding objective (GR_{SW}, FF_{SW}, FP_{SW}, VF_{SW}) as the fastest and the slowest growing fish will, respectively, be well above and well below the targeted weight. Consequently, there is a discrepancy between the recorded traits and their definition in the breeding goal. The main reason for this is that recording the traits at about the same body weight is labor-demanding and also stressful for the fish, as the fish need to be graded frequently so that the appropriate fraction of the largest fish can be slaughtered and measured at each grading event. For fish reared under natural environmental conditions, e.g., in floating net cages in the sea in which the seawater temperature and daylight vary over the year, introducing sample slaughter would also introduce substantial environmental differences and handling stress between the fish at the different slaughter events which may cause biased estimates of parameters and breeding values.

In Atlantic salmon estimates of genetic correlations between GR_{SA} and FF_{SA} are relatively high (0.34–0.74) (see **Appendix 2**). If these positive correlations reflect the corresponding genetic correlation between growth rate (GR_{SW}) and filet fat (FF_{SW}), simultaneous genetic improvement of the two traits may be difficult to achieve. To reduce the impact of this seemingly unfavorable genetic correlation, estimated breeding values for FF_{SA} maybe obtained by including body size of the fish as a covariate in the statistical model, or by pre-correcting the FF_{SA} records for body size. This would account for both environmental and genetic effects of body size on FF_{SA} and may therefore affect both the genetic and residual correlations of FF_{SA} with GR_{SA} and other traits. This was illustrated in two studies in Atlantic salmon where the genetic correlation between body weight (GR_{SA}) and filet fat (FF_{SA}) changed from positive to negative when FF_{SA} was accounted for body weight (from 0.45 to −0.22 (Rye and Gjerde, 1996) and from 0.45 to −0.10 (Vieira et al., 2007)). This illustrates the importance of having reliable estimates of the genetic correlation between the traits as defined in the breeding objective as this may have large effects on both the predicted responses of the traits under selection, the predicted correlated responses in other traits and on the relative weighting needed to obtain the desired gain in each of the traits.

For fish slaughtered at the same age estimates of genetic correlation between *GR* and *FF* are also found to be positive in Coho salmon, Arctic char, common carp, and sea bream, but negative in rainbow trout and close to zero in European whitefish (see **Appendix 2**). Between *GR* and *FP* both positive and negative correlations are reported, while negative correlations seem to be the most common of *FF* with *FP* and *VF*. For the magnitude of the few other genetic correlations reported in **Appendix 2** (those between *GR* and *VF* and between *FP* and *VF*) no clear picture can be drawn.

The objective of this study was to obtain reliable genetic parameter estimates for GR_{SW}, FF_{SW}, VF_{SW} and FP_{SW} by sampling and recording the traits at about the same body weight (*SW*). For comparison, the traits were also recorded on a different sample of sibs from the same families when slaughtered at the same age (GR_{SA}, FF_{SA}, VF_{SA} and FP_{SA}). The *SW* and the *SA* fish were reared in tanks at a land-based facility in which seawater temperature and natural light over the experimental period to provide as similar environmental conditions as possible for the *SW* fish slaughtered at the six different slaughter events.

MATERIALS AND METHODS

On request, authorities in Iceland stated that the recording of body weights of live fish does not require a special permit. The two other traits were recorded on dead fish. All fish was kept and managed according to Icelandic law.

Fish and Their Rearing

The Atlantic salmon in this study were from the breeding nucleus of Stofnfiskur in Iceland. The material used consisted

of 2 year-classes produced in fall 2008 (yc 1) and spring 2009 (yc 2) using a nested mating design where each female was mated to one male and each male to two females in most cases, but some males were mated with a single female only. Within each year class, all matings were completed over 4 weeks. Year-class (yc) 1 consisted of 106 fullsib families (offspring of 106 females and 68 males) and yc 2 of 100 families (offspring of 100 females and 52 males). From fertilization until start feeding the families were reared in separate hatching trays at Stofnfiskur family unit. The yc 1 families were startfed over a 11 days period from 20/4/2009 to 1/5/2009, while the families in yc 2 were startfed over 12 days from 10/11/2009 to 22/11/2009. From startfeeding until individual tagging of the fish, the families were reared separately in 1.5 m^2 tanks at Stofnfiskur family unit. At an average body weight of 15 g, a random sample of 100 fish from each fullsib family were individually tagged with PIT (Passive Integrated Transponder) tags deposited into the abdomen cavity of the fish. After tagging the fish were reared in a common tank until smoltification at an average body weight of 80 g. After smoltification, the tagged smolt of each year class was transported and reared in a common on-shore and in-door tank at Stofnfiskur breeding stations in Kalmanstjörn (yc 1) or Vogavík (yc 2). Rearing was under natural light and using borehole seawater with natural and stable salinity (ranging from 30 to 31‰ Kalmanstjörn and from 23 to 28‰ Vogavík) and temperature (ranging from 10 to 11°C in Kalmanstjörn and from 7.5 to 9°C in Vogavík). Genetic correlations between growth rate until an average body weight of 3 kg at these two farms have repeatedly found to be high (Jónas Jónasson pers comm.) and thus negligible genotype by environment interaction for growth. The feed used was commercial feed pellets containing 25% fat (22.9 MJ/kg) and 50 mg astaxanthin/kg (Vörur, 2020). The fish received ad-lib feeding adjusted to appetite.

Two Experimental Groups

The fish of each year-class were reared in one (yc 1) and four (yc 2) tank(s) until an average body weight of 2.5 kg, at which the fish of each year-class and family were divided randomly into two groups, one slaughtered at the same age (*SA*) and the other at about the same body weight (*SW*). All the *SA* group fish were slaughtered when they reached the average target body weight of about 4.6 kg, while the *SW* group fish were slaughtered at an individual target body weight of about 4.6 kg and thus at different ages.

For yc 1 the group sizes were 10 and 13 individuals per family for the *SA* and *SW* group, respectively; while for yc 2, the group sizes for both groups (*SA* and *SW*) were 15 individuals per family.

Slaughtering of the SA Group

The *SA* groups of both year-classes were reared in one tank from an average body weight of 2.5 kg to the desired harvest body weight and were harvested over 5–7 days; yc 1 889 to 904 days from first feeding (9335 to 9492°d) at an average body weight of 4.4 kg with a standard deviation of 1.1 kg, and yc 2 1024 to 1038 days from first feeding (8448 to 8564°d) at an average body weight of 4.6 kg with a standard deviation of 1.3 kg.

Sampling and Slaughtering of the SW Group

The *SW* yc 1 was reared in two tanks from an average body weight of 2.5 kg. After the third sampling from each of the two tanks, the biomass was sufficiently reduced to pool the fish into one tank (see **Table 1**). The *SW* yc 2 was reared in one tank from an average body weight of 2.7 kg until the end of the experiment.

In both year-classes, a fraction of the largest fish was slaughtered at five different slaughter events and the remaining fish at a sixth slaughter event over 148 (yc 1) and 188 (yc 2) days, and with 167 to 290 fish (yc 1) and 131 to 333 fish (yc 2) being slaughtered at each slaughter event (**Table 1**). The number of days between each slaughter event varied from 21 to 35 (yc 1) and from 30 to 47 (yc 2) days.

At the first slaughter event for both year classes, fish larger than 4.2 kg were slaughtered, while for the four following slaughtering events fish larger than 4.4 kg were slaughtered. In this way, the average targeted body weight of 4.6 kg (4.65 to 4.82 g in yc 1 and 4.64 to 4.87 kg in yc 2) was obtained for the five first slaughtering events. At the sixth and last slaughter event, the average body weight of the remaining fish was 4.05 kg in both year classes.

The fish to be slaughtered were sampled and kept in a separate tank for 1 week until being slaughtered by cutting the gills and bled before fileting. At each of these samplings, the body weight of some fish just below the set body weight threshold for slaughter were also recorded since the fish were subjectively sampled. These fish were not slaughtered at the actual slaughter event. The number of fish with body weight records just below the set threshold can be found as the difference between the number of recorded and slaughtered fish in **Table 1**. For yc 1 this number of fish was 83, 266, 192, 289, and 125, for slaughter event 1, 2, 3, 4, and 5, respectively; and similarly, for yc 2 218, 30, 91, 178, and 139 fish.

The body weights of the fish of a few random samples (five in yc 1 and two in yc 2) were obtained 4–6 days before some of the slaughter events, primarily to find the appropriate time for each slaughtering, but also to investigate if including or omitting these records from the statistical analyses have an effect on the parameter estimates. The number of individuals and dates of measure are given in **Table 1**.

All the sampled fish were anesthetized by manually picking up the fish from the tank and placing it into a 200-liter container with 100 ml of Phenoxyethanol.

For the *SW* group, the biomass (kg/m^3 seawater in the rearing tank) over the experimental period is shown in **Figure 1**. For yc 1 it was 13 at first recording and 18, 17, 15, 25 (two tanks merged into one tank), 13 and 5 kg/m^3 at each of the six slaughtering events, respectively; while for yc 2 it was 12 at first recording and 14, 14, 13, 11, 6, and 5 kg/m^3 at each of the six slaughtering events, respectively. Similarly, for yc 1 the fish density (no of fish/m^3) was 5.3 at first recording and 4.6, 3.7, 2.7, 1.5, 0.9, and 0.2 at each of the six slaughtering events, respectively; while for yc 2 it was 4.3 at first recording and 3.9, 3.3, 2.5, 1.5, 1.1, and 0.1 at each of the six slaughtering events, respectively. For the *SA* group, the biomass at slaughter was 18 kg/m^3 (yc 1) and 27 kg/m^3 (yc 2).

TABLE 1 | Descriptive statistics of the studied traits for each year-class and experimental group of the SW group at each sampling and slaughter date.

			Age		Body weight,kg		Growth rate, g/day			Filet fat, %		Filet pigment, mg/kg		Visceral Index		Body weight, kg		Growth rate, g/day	
Slaughter nr.	**Sample**	**Date**	**Days**	***N***	**Mean**	**SD**	**Mean**	**SD**	***N***	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Year-class 1																			
0	ST	07.03.2011	700	1276	2.44	0.64	3.49	0.91											
	RA	03.05.2011	748	93	2.48	0.68	3.31	0.91											
	RA	21.06.2011	797	92	3.39	0.90	4.26	1.13											
1	SL	05.07.2011	805	250	4.41	0.52	5.48	0.65	167	13.38	0.98	7.12	0.53	9.30	1.28	4.67	0.43	5.80	0.53
2	SL	09.08.2011	840	481	4.31	0.39	5.13	0.47	215	13.72	0.88	7.66	0.56	7.76	1.77	4.65	0.24	5.54	0.28
	RA	23.08.2011	860	101	4.15	0.70	4.82	0.82											
3	SL	30.08.2011	861	449	4.44	0.39	5.15	0.45	257	14.17	0.96	7.41	0.92	7.43	1.38	4.71	0.21	5.47	0.24
	RA	16.09.2011	884	97	4.55	0.64	5.15	0.72											
4	SL	04.10.2011	887	579	4.23	0.70	4.77	0.79	290	14.90	1.23	6.91	0.66	7.17	1.15	4.77	0.26	5.38	0.29
	RA	16.10.2011	911	54	4.13	0.71	4.53	0.79											
5	SL	01.11.2011	923	268	4.55	0.51	4.92	0.55	143	15.80	1.05	7.27	0.60	7.37	1.28	4.82	0.30	5.19	0.28
6	SL	30.11.2011	958	156	4.05	0.79	4.22	0.82	156	14.50	1.47	6.98	0.72	7.45	1.28	4.05	0.78	4.22	0.82
Year – class 2																			
0	SL	05.12.2011	1079	1418	2.73	0.77	2.53	0.71											
1	SL	31.05.2012	1142	349	3.75	1.11	3.28	0.97	131	15.51	1.03	7.94	0.51	6.26	0.87	4.85	0.62	4.26	0.54
2	SL	17.07.2012	1190	233	4.87	0.34	4.10	0.28	203	16.24	1.12	8.24	0.67	6.41	0.94	4.87	0.34	4.10	0.29
	RA	22.08.2012	1225	94	3.95	0.88	3.22	0.72											
3	SL	31.08.2012	1234	359	4.68	0.47	3.79	0.38	268	16.44	1.27	7.88	0.87	6.48	10.1	4.87	0.34	3.95	0.28
	RA	20.09.2012	1254	98	4.08	0.86	3.25	0.68											
4	SL	01.10.2012	1265	486	4.54	0.44	3.59	0.35	308	15.98	1.16	7.31	0.59	6.13	0.89	4.81	0.28	3.80	0.22
5	SL	31.10.2012	1295	282	4.35	0.37	3.36	0.29	143	16.72	1.39	6.83	0.66	6.79	1.03	4.64	0.17	3.59	0.13
6	SL	05.12.2012	1330	333	4.05	0.83	3.04	0.62	333	15.48	1.79	6.77	0.57	6.73	1.06	4.05	0.82	3.04	0.62

Sample abbreviations as follows: SD,standard deviation; ST,start when sorting the group for the trial; RA,random sample; SL,slaughter.

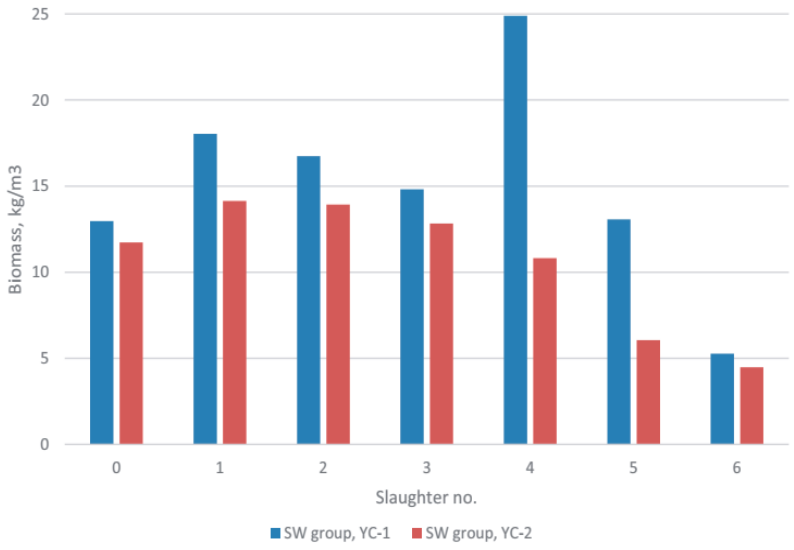

FIGURE 1 | Biomass for the SW group at the start (0) and at each of the six slaughter events of the 2 year-classes. For the SA group, the biomass at slaughter was 18 kg/m^3 (yc 1) and 27 kg/m^3 (yc 2).

Traits Recorded

For both the *SW* and the *SA* groups the following traits were recorded at slaughter for each of the 2 year classes: the round body weight (*BW* in kg), filet fat (FF_{SW}, FF_{SA}, in %), filet pigment (FP_{SW}, FP_{SA}, in mg/kg), and visceral weight (including liver, gut and intestinal fat) divided by the round body weight to obtain visceral index (VF_{SW}, VF_{SA} in %) as an indicator of visceral fat (Kause et al., 2007). For the *SW* group the body weight (*BW*, in kg) of all fish were recorded when the average body weight of the whole group was 2.4 kg (yc 1) and 2.7 kg (yc 2). Growth rate (GR_{SW}, GR_{SA}, in g/day) was calculated as round body weight divided by the number of days from the first feeding to slaughter.

Filet fat (FF_{SA}, FF_{SW}) and filet pigment (FP_{SA}, FP_{SW}) were measured on both filets in pre-rigor state. *FF* was predicted based on backscatter of light in the near-infrared spectra (NIR, wavelengths at 15 channels between 760 and 1040 nm). *FP* was predicted based on backscatter of visible light (VIS, wavelengths at 15 channels between 430 to 730 nm) the visual (VIS) spectra using the Qmonitor (TOMRA, 2020) installed at Stofnfiskur, Iceland (see next paragraph). These wavelength spectra were used as the explanatory (and predictor) variables, while the response variables were the chemically analyzed filet fat and filet pigment values of a homogenized sample of the whole filet without skin as the response variables (Folkestad et al., 2008). The average predicted filet fat and filet pigment value of both filets were used.

Prediction Model for Filet Fat and Filet Pigment

The prediction model for filet fat and filet pigment was developed based on data obtained from a sample of 24 Atlantic salmon weighing between 1 to 6 kg. The fish were from the same breeding nucleus population as the experimental groups (see section "Fish and Their Rearing"). The mean filet fat of the fish was 13.7% (standard deviation 2.1% units), and the mean filet pigment was 7.4 mg astaxanthin (standard deviation 1.4 mg/kg).

The prediction models were developed using *PLS* (Partial Least Squares) regression (Tormod Næs, 2002). Prediction error was reduced further by Canonical Partial Least Squares (CPLS) regression (Indahl et al., 2009) where additional information from each fish was included (round body weight, filet weight and visceral weight).

As the variation in the fat content within a filet is very high a better prediction model for filet fat, than using the average fat value of the filet, was obtained by using the fat content of five selected filet plug samples from each filet (a total of 120 plugs, each of approximately 15 mm in diameter) as the response variables and the NIR wavelengths spectra from the same locations as the plugs as the explanatory variables (Segtnan et al., 2009).

The fat content of each of the 120 plugs was obtained from a low-field nuclear magnetic resonance (H-NMR) instrument (Marin Ultra, 23 MHz, Oxford Instruments, United Kingdom) at Nofima, Ås and which are highly correlated to chemical analyzed fat values (Sørland et al., 2004).

The remaining part of each filet without skin was minced using a food blender, and a 30 g sample was analyzed for fat (%) (Soxhlet method), astaxanthin (mg/kg) and canthaxanthin (mg/kg) at Nofima, Sunndalsøra. The prediction model for filet fat of the whole filet was validated using the chemically analyzed fat values of 24 filets (one filet from each fish).

The summary statistics for the prediction models for filet fat and filet pigment in this study and the filet fat model developed in

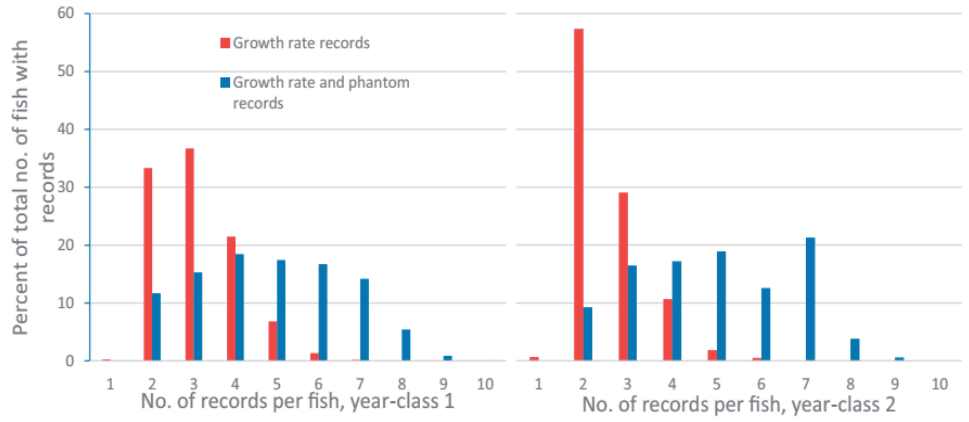

FIGURE 2 | Percent of the total number of fish with growth records with 1 or up to 10 repeated growth records, or 1 or up to 10 growth and phantom records for each of the 2 year-classes.

Segtnan et al. (2009) where the plug sampling methodology was described are shown in **Appendix 1**. For filet fat in the whole filet, the *PLS* based prediction model had a root mean square error of prediction (RMSEP) of 2.02%-units as compared to 1.88%-unit for the *CPLS* model. For filet pigment, the *RMSEP* was 0.84 mg/kg using PLS regression and did not improve when using *CPLS* regression.

Statistical Methods

In the *SW* group, the faster-growing fish were slaughtered before the slower-growing fish. Hence, BW_{SW} and its corresponding trait value GR_{SW} were truncated trait values recorded at six different time points over the 6 months experimental period, but with only one record per fish for most of the fish. Therefore, as the fish at each time point were slaughtered at about the same body weight, mean GR_{SW} at each time point will decrease over time. Consequently, if only the sampled fish were included in the analysis at each time point, the parameter estimates for GR_{SW} and other traits (FF_{SW}, FP_{SW}, VF_{SW}) would be biased.

Hence, a statistical model was needed which accounted for the body weight distribution of all fish present at each of the six sampling events. The available data for such a model was the BW_{SW}, FF_{SW}, VF_{SW} and FP_{SW} records of the fish slaughtered at each of the six slaughter events, the body weight records of the sampled but not slaughtered fish, and the (ID of) remaining fish in the tank(s) at each slaughter event and known to be smaller than any of the slaughtered fish.

For this purpose, a Bayesian multivariate model for (potentially) truncated Gaussian traits (Ødegård et al., 2010) implemented in the Gibbs sampling module in DMU (Jensen et al., 2014) was used. The procedure simulates left-censored growth rate phenotypes for the fish with no GR_{SW} records at each of the six slaughter events, sampled from a truncated normal distribution, upwardly truncated at the set body weight threshold.

Estimates of (co)variances for the random effects and BLUE-estimates for the different levels of the fixed effects for the studied traits were obtained from a multi-trait animal model with eight traits (GR_{SW}, FF_{SW}, FP_{SW}, VF_{SW}, GR_{SA}, FF_{SA}, FP_{SA} and VF_{SA}). GR_{SW} was a left-censored trait (including a few recorded but not slaughtered individuals below the threshold) with at least two and up to ten records per fish (**Figure 2**).

Yc 1 and yc 2 were first analyzed separately. Estimated (co)variances for the traits were similar and did not differ significantly between the 2 year-classes. Therefore, the datasets from both year-classes were analyzed jointly. In matrix notation the model may be written as:

$$\boldsymbol{Y} = \begin{bmatrix} \boldsymbol{Y}_{1-7} \\ \boldsymbol{Y}_{8} \end{bmatrix} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{Mc} + \begin{bmatrix} \mathbf{0} \\ \mathbf{S} \end{bmatrix} \boldsymbol{r} + \boldsymbol{e} \qquad (1)$$

The vector $\mathbf{Y}_{1-7}$ represented the seven traits GR_{SA}, FF_{SA}, FP_{SA}, VF_{SA}, FF_{SW}, FP_{SW}, VF_{SW} with only one record per animal which was not censored since they were not subject to selection, while the vector $\mathbf{Y}_8$ represented the trait GR_{SW} which was a left-censored longitudinal trait with two to ten repeated GR_{SW} records (including the censored phenotypes). For trait $\boldsymbol{Y}_{1-7}$ the fixed effects included the combination of year-class (2 year-classes), tank (seven tanks) and sex (males and females). The fixed effects for $\mathbf{Y}_8$ were year-class, tank, sampling group (23 groups) and sex; the vector $\mathbf{a} \sim \mathbf{N}(\mathbf{0}, \mathbf{A} \otimes \mathbf{G_0})$ included the additive animal genetic effects for each of the studied traits where $\boldsymbol{A}$ was the numerator relationship matrix constructed from the pedigree of the parents and grandparents and $\mathbf{G_0}$ was the additive genetic (co)variance matrix; the vector $\mathbf{c} \sim \mathbf{N}(\mathbf{0}, \mathbf{I} \otimes \mathbf{C_0})$ included the effects common to fullsibs other than additive genetics and $\mathbf{C_0}$ was the (co)variance matrix of effects common to full-sibs; the vector $\mathbf{r} \sim \mathbf{N}(\mathbf{0}, \mathbf{I}\sigma^2_{\mathbf{r}})$ included the individual repeatability effects due to two or more repeated GR_{SW} records on the same fish; $\mathbf{e} \sim \mathbf{N}(\mathbf{0}, \mathbf{I} \otimes \mathbf{R_0})$ was a vector of random residuals and $\mathbf{R_0}$ was the residual (co)variance matrix.

For each of the 2-year classes, the *SA* and *SW* traits were recorded on different individuals, resulting in independent

residuals between traits in the *SA* and the *SW*groups, and thus $\mathbf{e} \sim \mathbf{N}(\mathbf{0}, \mathbf{R_0})$, where:

$$\mathbf{R_0} = \begin{bmatrix} \mathbf{R_{0_{1-4}}} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{R_{0_{5-7}}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma^2_{e_8} \end{bmatrix}$$

where $\mathbf{R_{0_{1-4}}}$was the residual (co)variance matrix of the four traits in the *SA* group, $\mathbf{R_{0_{5-7}}}$ was the residual (co)variance matrix for the traits FF_{SW}, FP_{SW}, VF_{SW}in the *SW* group and $\sigma^2_{e_8}$ was the residual variance of GR_{SW}. GR_{SW} was a longitudinal trait, while all other traits were cross-sectional. Hence, this method did not allow residual correlations between GR_{SW} and other traits in the *SW* group to be estimated. However, the advantage of longitudinal modeling of GR_{SW} was that it accounts for the non-random slaughter of the fish at each of the six slaughtering events.

The matrices **X**, **Z** and **M,** are incidence matrices that assign the observations to their appropriate fixed effect, random additive genetic and common fullsib effects, respectively. The matrix **S** assigns the phenotypes of repeatability effect to the trait GR_{SW} (not relevant for the other traits). For an individual *I* still alive at time point *j* with body weight below the sampling threshold, the growth rate phenotype was drawn from the truncated normal distribution (TN) as:

$$\boldsymbol{Y}_{\mathbf{8},ij} \sim \mathbf{T}N\left(\mathbf{X}_{8i}\mathbf{b}+\mathbf{Z}_{8i}\mathbf{a}+\mathbf{M}_{8i}\mathbf{c}+\mathbf{S}_i\mathbf{r}, \sigma^2_{e_8}, -\infty, \frac{\mathbf{TW_j}}{\mathbf{t}_{ij}}\right)$$

where the growth phenotype was truncated in the interval − to $\frac{\mathbf{TW_j}}{\mathbf{t}_{ij}}$, where TW_j was the threshold weight at time ***j*** (the body weight of the smallest slaughtered fish) and $\mathbf{t}_{ij}$ was the age (days from start feeding) for fish ***i*** at time ***j***. The TN distribution has also fixed and random effects for individual ***i***.

The model was run for 2.017.200 rounds, discarding the first 10.000 samples as burn-in, with a sample interval of 100 rounds; thus the estimated (co)variances were based on 20.072 rounds retained from the Monte Carlo Markov Chain (MCMC) chain. Convergence was evaluated using Raftery and Lewis convergence diagnostics (Raftery and Lewis, 1992) using the package Coda (Plummer et al., 2018) in the statistical program R (R Development Core Team, 2018). Raftery and Lewis reveal how many rounds from the MCMC are needed by evaluating 2.5% quantile from the chain at given precision with the probability 0.95. If the precision was set to 0.02, the desired number of rounds was lower than 20.072 for all parameters. If the precision was set to 0.1 the following parameters σ^2_{FFSA}, $\mathbf{h}^2_{FFSA}$, $\mathbf{h}^2_{FPSW}$, $\mathbf{r}_{GRSA,FPSA}$, $\mathbf{r}_{GRSA,FFSW}$ needed more rounds.

Heritability $\mathbf{h^2}$ was calculated as the additive variance $\sigma^2_\mathbf{a}$ divided by the phenotypic variance $\sigma^2_\mathbf{p}$ denoted as

$$\mathbf{h}^2 = \frac{\sigma^2_\mathbf{a}}{\sigma^2_\mathbf{p}}$$

Where $\sigma^2_\mathbf{p} = \sigma^2_\mathbf{a}+\sigma^2_\mathbf{c}+\sigma^2_\mathbf{e}$; $\sigma^2_\mathbf{a}$ was the additive genetic variance, $\sigma^2_\mathbf{c}$ was the variance of the effect common to fullsibs, and $\sigma^2_\mathbf{e}$ was the residual variance. For the trait GR_{SW} the $\sigma^2_\mathbf{p}$ also contains the repeatability variance $\sigma^2_\mathbf{r}$ so the phenotypic variance becomes.

$$\sigma^2_\mathbf{p} = \sigma^2_\mathbf{a}+\sigma^2_\mathbf{c}+\sigma^2_\mathbf{e}+\sigma^2_\mathbf{r}$$

The proportion of the variation due to the effect common to fullsibs c^2 was calculated as the variance common to fullsibs $\sigma^2_\mathbf{c}$ divided by the phenotypic variance $\sigma^2_\mathbf{p}$ defined as

$$\mathbf{c}^2 = \frac{\sigma^2_\mathbf{c}}{\sigma^2_\mathbf{p}}$$

The genetic correlation between trait 1 and 2 $(\mathbf{r_{g1,2}})$, the correlation of the effect common to fullsibs between trait 1 and 2 $(\mathbf{r_{c1,2}})$, and the residual correlation between trait 1 and 2 $(\mathbf{r_{e1,2}})$ were calculated as

$$\mathbf{r}_{g1,2} = \frac{\sigma^2_{g12}}{\sigma_{g1}\sigma_{g2}} \quad \mathbf{r}_{c1,2} = \frac{\sigma^2_{c12}}{\sigma_{c1}\sigma_{c2}} \quad \mathbf{r}_{e1,2} = \frac{\sigma^2_{e12}}{\sigma_{e1}\sigma_{e2}}$$

Effects of Pre-correcting FF_{SA} for Body Weight

It is of interest to investigate if traits recorded at the same age (*SA*) can be adjusted to obtain parameter estimates comparable to those obtained for trait recorded at the same body weight (*BW*). In this paper, we limit this to a small investigation for the trait *FF* with a pre-correction of the observed FF_{SA} trait values for their corresponding BW_{SA} records. An in-depth study of how to best perform this will be the objective of another paper.

First, the regression coefficient of FF_{SW} on BW_{SW} was obtained from the following linear model, separately for each of the 2 year-classes:

$$FF_{SA} = \beta_0 + \beta_1 BW_{SA} + e \tag{2}$$

This regression coefficient (β_1) was used to generate the pre-corrected phenotype $preFF_{SA}$ as follows, for each of the 2 year-classes:

$$preFF_{SA} = FF_{SA} - \beta_1 BW_{SA} \tag{3}$$

The genetic correlation of $preFF_{SA}$ with FF_{SW}, GR_{SW} and GR_{SA} were obtained from bivariate animal models with the same fixed effect as in Model 1.

RESULTS

Descriptive Statistics

The total number of slaughtered individuals with records for all the studied traits were 1228 (yc 1) and 1386 (yc 2) for the *SW* group and 965 (yc 1) and 1412 (yc 2) for the *SA* group. In addition, there were 48 (yc 1) and 32 (yc 2) fish with growth records that died before reaching the targeted body weight for slaughter. The percentage of fish in the *SW* group lost due to mortality, and typographical errors were 4.2% (yc 1) and 7.6% (yc 2) of the total number of fish at the start (*ST*) of the sampling (see **Table 2**). For the *SA* group, the corresponding numbers were 2.1% (yc 1) and 1.2% (yc 2).

TABLE 2 | Descriptive statistics for the four studied traits of each year-class and experimental group[1].

		Growth, g/day			Visceral index, %			Filet pigment, mg/kg			Filet fat, %		
Year-class	**Group**	***N***	**Mean**	**CV × 100**	***N***	**Mean**	**CV × 100**	***N***	**Mean**	**CV × 100**	***N***	**Mean**	**CV × 100**
1	SA	961	4.96	23.4	964	6.13	18.3	965	7.29	11.8	965	13.79	11.5
1	SW	3904	4.43	24.2	1276	7.66	19.8	1260	7.22	10.2	1228	14.39	9.2
2	SA	1412	4.47	28.4	1414	5.28	15.9	1412	7.53	11.3	1412	17.29	12.8
2	SW	3647	3.31	24.8	1418	6.46	15.5	1385	7.44	11.6	1386	16.02	8.9

[1] *For the SA group, the mean round body weight (CV × 100) at slaughter was 4.40 kg (23.4) for yc 1 and 4.60 kg (28.3) for yc 2.*

The descriptive statistics of the four studied traits in **Table 2** show that the mean observed growth rate of yc 1 was higher than of yc 2 for both the *SA* and the *SW* group, probably because yc 1 was reared at a higher water temperature than yc 2 (see section "Fish and Their Rearing"). For visceral index and filet fat, some differences in mean values were observed between the *SA* and the *SW* groups, within and across the 2 year-classes, but with no clear trend. Average filet fat was higher in yc 2 than in yc 1 for both the *SA* (3.5%-units higher) and the *SW* (1.6%-units higher) group. For the *SA* group this may be due to the about 200 g higher mean body weight of yc 2 (4.60 kg, CV 28.3%) than of yc 1 (4.40 kg, CV 23.4%), while for *SW* the overall mean body weight of the slaughtered fish was 4.61 kg for yc 1 and 4.68 for yc 2 with a CV 8.0% for yc 1 and 9.1% for yc 2. Mean values for filet pigment were very similar for the two groups within and across the 2 year-classes.

Furthermore, **Table 2** shows that the coefficient of variation (*CV*) of growth rate was similar for the *SA* and the *SW* groups. Very similar *CV* for the two groups was also observed for visceral index and filet pigment of each year-class, while for filet fat a somewhat higher *CV* was found for the *SA* group than for the *SW* group. For filet pigment means and *CV* for the *SA* and *SW* groups were very similar within and across the 2 year-classes.

Table 1 shows that the mean body weight of the *SW* group at the five first slaughtering events ranged from 4.65 to 4.82 kg (yc 1) and from 4.64 to 4.87 kg (yc 2), and thus close to the set desired body weight of 4.6 kg. The *CV* of body weight at each slaughtering event varied from 4.5 to 9.0% (yc 1) and from 3.6 to 12.8% (yc 2) for slaughter events one to five. The mean body weight of the fish slaughtered at the sixth and last slaughtering event was lower (4.05 kg for both year-classes) as all the remaining fish were slaughtered at this slaughter event and therefore with a larger *CV* (19.3% for yc 1 and 20.4% for yc 2) than for the fish slaughtered at the five first slaughtering events. *CV* of filet fat varied from 6.6 to 8.3% (yc 1) and from 6.7 to 8.3% (yc 2) for slaughter event one to five but was higher at the sixth and last slaughter events (*CV* 10.1% for yc 1 and 11.5% for yc 2) most likely due to the larger variation in body weight. For each year-class, the filet pigment was quite similar over the six slaughter events and with quite similar standard deviations and thus different *CV*s (*CV* 6 to 12%), while the visceral index at each of the six slaughter events had similar standard deviations but different means and thus different *CV*s (*CV* 16 to 26%).

For the *SW* group, the mean observed filet fat percentage increased throughout the slaughter events while the mean observed growth rate decreased (**Table 1**). This indicates that slow growers add more fat in the filet than fast growers but could also be interpreted as filet fat generally increases with age.

For yc1 there were in total 3904 growth records and 6139 growth and phantom records, and for yc 2 3647 growth records and 6963 growth and phantom records. Of the total number of fish with growth records 91.5% (yc 1) and 97.0% (yc 2) had two to four repeated growth records (**Figure 2**), while 45.4% (yc 1) and 42.9% had two to four growth and phantom records (**Figure 2**).

Observed and Estimated Growth Rate at Each Slaughter Event of the SW Group

In **Figure 3**, the decreasing mean observed growth rate over the six slaughter events showed that the fastest-growing fish were slaughtered first. The difference between the mean observed and the mean estimated growth rate is due to the slaughter and body weight recording of only the largest fish at each slaughter event, which the statistical model is meant to account for through assigning phantom growth rate phenotypes for the fish with no body weight record at each of the five first slaughter events. The estimated growth curve is expected to equal the growth curve that would be realized if the body weight of all or a random sample of the fish (i.e., not selected on body size) was recorded at each slaughter event.

Heritability

Table 3 shows that the estimated heritability for the same trait in the two groups was quite similar whether recorded at the same age (*SA*) or the same body weight (*SW*); of medium magnitude (0.20–0.37) for *GR*, *FF* and *VF*, but lower for *FP* (0.11–0.16).

Genetic and Residual Correlations

Estimates of genetic and residual correlations among the traits are given in **Table 3**. The genetic correlation between the same trait in the two groups was high for *GR* (0.91 ± 0.05) and *VF* (0.86 ± 0.05) indicating that these traits are not sensitive to whether recorded at the same age (*SA*) or the same body weight (*SW*), and will thus result in quite similar ranking of the families whether recorded at *SW* or *SA*. For *FF*, the genetic correlation was of medium magnitude (0.45 ± 0.17) and rather low for *FP* (0.13 ± 0.27) which implies substantial reranking of families for each of these traits when recorded at *SW* or *SA*.

Within each of the two groups, the genetic correlation between *GR* and *FF* changed from positive (0.59 ± 0.14) for the *SA* group to negative (-0.45 ± 0.17) for the *SW* group, while the genetic correlation between *GR* and *FP* changed from negative

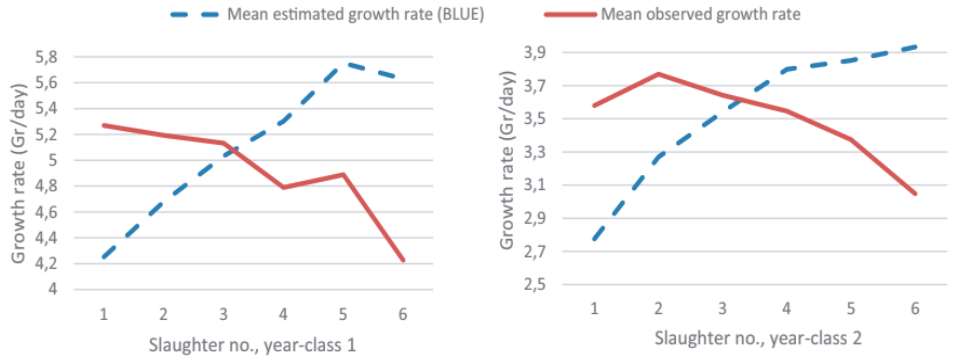

FIGURE 3 | The mean observed growth rate of all the recorded fish (the slaughtered ones and those close to the set body weight threshold for slaughtering) and the BLUE-estimates for the mean growth rate of all fish (the recorded ones and the not recorded fish that were still alive in the tank) at each of the six slaughter events for each of the 2 year-classes.

TABLE 3 | Estimates of heritability of the studied traits (on the diagonal) and genetic (below the diagonal) and residual (above the diagonal) correlations between the traits based on the data from both year classes.

	FF_{SA}	FP_{SA}	VF_{SA}	GR_{SA}	FF_{SW}	FP_{SW}	VF_{SW}	GR_{SW}
FF_{SA}	0.23 ± 0.08	−0.35 ± 0.03	0.04 ± 0.05	0.69 ± 0.03	–	–	–	–
FP_{SA}	−0.37 ± 0.23	0.11 ± 0.04	−0.08 ± 0.04	−0.16 ± 0.04	–	–	–	–
VF_{SA}	−0.12 ± 0.19	0.08 ± 0.20	0.37 ± 0.06	−0.21 ± 0.05	–	–	–	–
GR_{SA}	0.59 ± 0.14	−0.33 ± 0.22	−0.13 ± 0.16	0.33 ± 0.08	–	–	–	–
FF_{SW}	0.45 ± 0.17	−0.03 ± 0.23	−0.17 ± 0.15	−0.35 ± 0.18	0.20 ± 0.04	−0.20 ± 0.03	−0.05 ± 0.03	0.41 ± 0.02
FP_{SW}	0.26 ± 0.24	0.13 ± 0.27	0.09 ± 0.19	0.58 ± 0.17	−0.38 ± 0.20	0.16 ± 0.05	−0.13 ± 0.04	−0.01 ± 0.03
VF_{SW}	−0.14 ± 0.20	0.06 ± 0.20	0.86 ± 0.05	0.14 ± 0.17	−0.45 ± 0.13	0.16 ± 0.20	0.35 ± 0.06	−0.06 ± 0.03
GR_{SW}	0.44 ± 0.18	−0.31 ± 0.23	−0.09 ± 0.16	0.91 ± 0.05	−0.45 ± 0.17	0.62 ± 0.16	0.19 ± 0.17	0.35 ± 0.09

(−0.33 ± 0.22) for the *SA* group to positive (0.62 ± 0.16) for the *SW* group. Similarly, the genetic correlation between *GR* and *VF* was not significantly different from zero but changed from slightly negative (−0.13 ± 0.16) for the *SA* group to slightly positive (0.19 ± 0.17) for the *SW* group. Within both groups, the genetic correlation of *FF* with *FP* and *VF* was medium to low negative but not significantly different from zero, while those between *FF* and *VF* were low but positive but also not significantly different from zero.

The residual correlations between *FF*, *FP* and *VF* within each of the two experimental groups were low, while that between *GR* and *FF* was relatively high in the *SA* group (0.69 ± 0.03) and somewhat lower in the *SW* group (0.41 ± 0.02).

The low residual correlation between *FF* and *FP*, in both the *SA* (−0.35) and the *SW* (−0.20) groups, shows that these traits to a large extent were independently predicted. Most likely this is because the *FP* and *FF* values were obtained based on two different VIS and NIR wavelength spectra, respectively; and that the response variable in the prediction model for *FP* was the chemical analyzed pigment and not the visual filet color.

Effect Common to Fullsibs

Table 4 shows that the effect common to fullsib as a proportion of the phenotypic variance was rather low, being highest for GR_{SW} (0.14 ± 0.04), FF_{SA} (0.12 ± 0.04) and GR_{SA} (0.12 ± 0.04).

The fullsib (family) correlations between the same trait in the two groups were positive (**Table 4**). The correlations between different traits within the *SA* and *SW* groups (**Table 4**) were similar except for *FF* and *GR* which changed from strongly positive (0.78 ± 0.11) in the *SA* group to close to zero within the *SW* group (−0.09 ± 0.27). The correlation between *FP* and *GR* changed from negative in *SA* (−0.37 ± 0.22) to positive in *SW* (0.47 ± 0.20). Therefore, the fullsib effect correlations between these traits seem to be sensitive to whether phenotypes are recorded at the same age or about the same body weight.

Pre-correction of the Quality Traits

The genetic correlation between $preFF_{SA}$ and GR_{SA} was 0.05 ± 0.18 as compared to the much higher genetic correlation of 0.69 ± 0.03 between FF_{SA} and GR_{SA} and the much lower genetic correlation of −0.45 ± 0.17 between FF_{SW} and GR_{SW}. In addition, the genetic correlation between $preFF_{SA}$ and FF_{SW} was 0.81 ± 0.09 as compared to the much lower genetic correlation of 0.45 ± 0.17 between FF_{SA} and FF_{SW}. Consequently, pre-correction of the FF_{SA} records for body weight brought the genetic correlation between *FF* and *GR* recorded at the same age closer to the genetic correlation between the same two traits when recorded at the about the same body weight.

TABLE 4 | The effect common to fullsib as a proportion of the phenotypic variance (on the diagonal) and the correlation between the trait for this effect.

	FF_{SA}	FP_{SA}	VF_{SA}	GR_{SA}	FF_{SW}	FP_{SW}	VF_{SW}	GR_{SW}
FF_{SA}	0.12 ± 0.04	–	–	–	–	–	–	–
FP_{SA}	−0.59 ± 0.17	0.07 ± 0.02	–	–	–	–	–	–
VF_{SA}	0.21 ± 0.28	−0.19 ± 0.27	0.06 ± 0.03	–	–	–	–	–
GR_{SA}	0.77 ± 0.12	−0.37 ± 0.23	0.17 ± 0.28	0.12 ± 0.04	–	–	–	–
FF_{SW}	0.50 ± 0.22	−0.36 ± 0.26	−0.07 ± 0.31	−0.03 ± 0.28	0.05 ± 0.02	–	–	–
FP_{SW}	0.12 ± 0.23	0.31 ± 0.22	0.06 ± 0.29	0.39 ± 0.20	−0.34 ± 0.24	0.08 ± 0.03	–	–
VF_{SW}	0.16 ± 0.28	−0.12 ± 0.27	0.70 ± 0.18	0.33 ± 0.28	−0.28 ± 0.28	0.06 ± 0.28	0.06 ± 0.03	–
GR_{SW}	0.65 ± 0.16	−0.34 ± 0.22	0.21 ± 0.27	0.87 ± 0.08	−0.11 ± 0.27	0.48 ± 0.19	0.38 ± 0.27	0.14 ± 0.05

DISCUSSION

Genetic Parameters

The objective of this study was to obtain reliable genetic parameters of growth rate (*GR*), filet fat (*FF*), visceral fat (*VF*) and filet pigment (*FP*) when these traits were recorded on fish slaughtered at about the same body weights (*SW*) and varying age, and compare these with the parameter estimates of the same traits when recorded on their sibs at the same age (*SA*) and thus at different body weights. The heritability of each trait recorded at *SW* and *SA* were similar. However, the genetic correlations between the same trait in the *SA* and *SW* groups were moderate for *FF* (0.45±0.17) and low for *FP* (0.13±0.27). Also, some of the genetic correlation estimates changed sign whether recorded at *SW* or *SA*; between *GR* and *FF* 0.59 ± 0.14 for *SA* vs. −0.45 ± 0.17 for *SW*, between *GR* and *FP* −0.33 ± 0.22 for *SA* vs. 0.62 ± 0.16 for *SW*, and between *GR* and *VF* −0.13 ± 0.16 for *SA* vs. 0.19 ± 0.17 for *SW*. As the parameter estimates were consistent across the 2 year-classes, these results strongly suggest that *FF* and *FP* should be viewed as different traits and will cause substantial reranking of families when tested both at *SA* and *SW*. The moderately positive genetic correlation between *GR* and *FF* recorded at the same age (*SA*) agree well with published results for Atlantic salmon as well as for several other farmed fish species (see **Appendix 2**).

The low Genetic correlation between filet fat recorded at *SA* and *SW* and filet pigment recorded at *SA* and *SW*, strongly indicate that if these traits are directly selected for in a breeding program, the time of their recording (*SA* or *SW*) is highly relevant. As growth rate is an important trait in all selective breeding programs, selection for increased growth rate will likely result in commercially farmed fish being slaughtered at younger ages with each successive generation, potentially also altering the mean phenotypes and the genetics of the quality traits at the time of slaughter. This may complicate efficient selection for carcass quality traits. If selection is practiced for increased growth rate only, the genetic correlations of growth rate with the quality traits obtained at *SW* reveals likely their correlated effect when the fish are slaughtered at about the same body weight.

The relatively high genetic correlation between GR_{SA} and GR_{SW} (0.91 ± 0.05) indicates that growth rate is largely the same trait whether recorded at *SW* or *SA*. For growth the genetic correlation between body weights measured on the same animals at different ages and thus different body weights were found to be high when measured near in time (within a few months), but lower when measured further apart (Gjerde et al., 1994; Powell et al., 2008), indicating that growth should be measured at body weight as defined in the breeding objective.

Importance and Breeding Objective of Quality Traits in Atlantic Salmon

Production of an Atlantic salmon with more body fat than required from a marketing point of view should be avoided as deposition of fat requires more energy than deposition of protein (Knap and Kause, 2018), and as a fatty fish is likely also to be more costly to produce depending on the relative price of the fat and protein feed ingredients. A theoretical calculation shows that if the body fat of a salmon can be reduced by 1%-unit, the energy need of the fish could be reduced by about 0.4 MJ/kg, corresponding to a 0.034 reduction in *FCR* for a feed with 24.2 MJ/kg (T. Åsgård, pers. Comm), which for the Norwegian salmon industry (1.4 billion tons in 2019) amounts to about 50 000 tons of feed.

The breeding objective for *FF* depends foremost of the desired filet fat level in the most important salmon market(s), at what body size the fish are and will be harvested in the future as *FF* increases with body weight, and the present genetic potential for *FF* deposition of the animals in the actual breeding nucleus population. Given that selection for increased *GR* will result in an earlier harvest of fish at about the same body weight, it may be concluded that due to the negative genetic correlation between GR_{SW} and FF_{SW} (−0.45 ± 0.17), as well as between GR_{SA} and FF_{SW} (−0.35 ± 0.18), selection for increased *GR* is more likely to give a favorable correlated response in *FF* (i.e., a reduction) than the opposite. Consequently, *FF* may not need to be recorded or selected for unless the filet fat level becomes too low. However, by recording *FF* it becomes possible to reduce *FF* faster than possible through a correlated response through selection for increased *GR*, which may also be favorable from a feed efficiency trait point of view (Kause et al., 2016).

VF must be considered as a waste product but should not be reduced to a level with a negative effect on the fitness of the fish. For instance, reduced *VF* may affect reproduction as *VF* (and *FF*) is mobilized during sexual maturation (Aksnes et al., 1986), and the effect on reproduction may become larger if *FF* is also reduced. The low negative genetic correlation between GR_{SW} and VF_{SW} (0.19 ± 0.17) indicates that selection for increased *GR* will result in a modest but unfavorable correlated response in *VF*. Consequently, to obtain a reduction in *VF* will require

VF being recorded so that directional selection against this trait can be applied.

The most likely breeding objective for *FP* is to increase the retention efficiency of the carotenoids in the feed, and thus allow for the production of a fish with sufficiently high *FP* using a cheaper feed with less carotenoids, or for a more pigmented filet to obtain a higher price (Steine et al., 2005; Alfnes et al., 2006). However, during the last years, the economic value of *FP* has been reduced as costs associated with pigment in the feed has been reduced substantially and accounts for only 1.1–3.6% of the feed costs (Cargill) as compared to 15%, 15 years ago (Steine et al., 2005; Alfnes et al., 2006). Also the relatively high genetic correlation between GR_{SW} and FP_{SW} (0.62 ± 0.16) strongly indicates that selection for increased growth rate will result in a favorable correlated response in *FP* and also with a low but most likely favorable genetic correlation of FP_{SW} with both FF_{SW} and VF_{SW}.

Reliability of the Parameter Estimates

An important assumption for the above discussion is that the parameter estimates for the traits recorded at *SW* are both unbiased and accurate; i.e., that the Gibbs sampling procedure managed to account for the selection and recording of only the largest fish at five of the six slaughter events, and that the number of recorded fish at each event is sufficiently high to allow the Gibbs procedure to work properly.

The purpose of harvesting only the largest fish at five of the six slaughter events was to obtain the three carcass quality trait records at a body weight which is more in line with the most likely breeding objective of these traits, i.e., at about the same body weight, as compared to recording the traits at the same age as is the practice in today's selective breeding programs. The mean observed and estimated growth rate at each slaughter event (**Figure 3**) indicate that the Gibbs sampling procedure, to a large extent, managed to account for the culling on body weight. This is also supported by the fact that excluding the body weight (i.e., the GR_{SW}) records of the approximately 100 fish randomly sampled prior to slaughter event 1, 3, 4 and 5 (yc 1) and 3 and 4 (yc 2) (see **Table 1**) changed the parameter estimates only marginally. The effect of this culling for body weight on the quality traits cannot be accounted for in the same manner as for GR_{SW} but only through their correlation to GR_{SW}. Consequently, GR_{SW} is the only trait that can be modeled as a censored trait, and with only the overall mean as a fixed effect in the model for each of the quality traits. Therefore, for each of the quality traits a figure similar to **Figure 3** for GR_{SW} is not possible to produce. To what degree the correlations of growth trait with the quality traits are sufficient to produce unbiased parameter estimates for the latter traits can only be inferred using stochastic simulation where the true genetic (co)variances among the traits are known.

The unbiasedness of the estimated parameters for the traits of the *SW* group may be affected by changes in the rearing conditions (e.g., water temperature, feed, biomass and fish density) over the six slaughter events as these may have an effect on what degree culling with respect to body weight was properly accounted for through the Gibbs sampling procedure (see section "Rearing Conditions"). The accuracy of the estimated parameters for these traits depends on the number of slaughter events and the number and proportion of the fish slaughtered at each event. Moreover, since each fish in the *SW* group had at least two growth records, a repeatability effect could be estimated for the GR_{SW} trait, while no such effect could be estimated for the quality traits in the *SW* group. Given this, residual covariance of GR_{SW} with each of the three quality traits are difficult to estimate since GR_{SW} has many residuals per fish while each of the quality traits has only one. Hence, the residual term for GR_{SW} should be interpreted differently than for the other traits in the *SW* group. The unbiasedness and accuracy of the parameters can only be inferred from a well-designed stochastic simulation study where the true parameters are known.

Rearing Conditions

The fish in the *SA* group of each of the 2 year-classes were all slaughtered at the same time, and thus influenced by the same environmental rearing conditions until being slaughtered and the traits recorded. This is in contrast to the fish in the *SW* group for which the trait records were obtained at six different slaughter events over 6 months and thus being influenced by varying rearing conditions that may have had a different effect on each of the recorded traits. If these environmental effects were not properly accounted for by the Gibbs sampling procedure, this might have resulted in biased parameters. In this study water temperature and salinity was very stable over the entire experimental period, type of feed was the same and feed was given according to the predicted biomass over time. However, both biomass (kg/m^3) and fish density (no. of $fish/m^3$) varied over the six slaughter events with a possible effect on the growth as well as on the quality traits of the *SW* fish. These possible effects cannot be accounted for *per se* in the present data or using other data sources due to a lack of such published effects on the traits. In most studies where the effect of tank size and fish density on growth is evaluated, larger tanks and lower densities result in better growth (Refstie and Kittelsen, 1976; Espmark et al., 2017). Having a low number of fish in a tank can revel strong social hierarchies with effect on growth (Ranta and Pirhonen, 2006) and with a possible effect on the growth rates in particular the two last slaughter events. The effect of changes in the rearing environment on the growth of the fish in the *SW* group was sought to be accounted for by including the starting point and the six slaughter events (first column of **Table 1**) as a fixed effect in the statistical model (which also accounts for the age of the fish which may impact both their body composition and growth). Due to the relatively stable rearing conditions in the present study, we are confident that the Gibbs sampling procedure to a large extent managed to account for the relatively strong culling for body weight at five of the six slaughter events as well as for the relatively minor changes in environmental conditions over the experimental period. Performing a similar experiment, e.g., in a net-cage in

the sea in which the fish are exposed to a much larger change in the water temperature with a strong effect on growth rate would probably have resulted in less reliable parameters for traits in the *SW* group.

Recording the Quality Traits at SA or SW

Recording carcass quality traits at the same age of the fish is much less labor demanding than recording them at about the same body weight. However, the latter procedure is more in line with how quality traits should ideally be defined in the breeding objective. Therefore, if some carcass quality traits are to be directly selected for in a selective breeding program the question that remains to be answered is whether genetic parameters and breeding values for traits recorded on fish at the same age or about the same body weight are comparable.

In some breeding programs, an adjustment of the quality trait records for body weight is performed, e.g., by including body weight as a covariate for each quality trait, or by pre-correcting their phenotypes as exemplified for filet fat in chapter 2.8. These results strongly indicate that pre-correction of filet fat for body weight brings the genetic correlation between $preFF_{SA}$ with GR_{SW} closer to the genetic correlation between FF_{SW} and GR_{SW}, and that pre-correcting the FF_{SA} records for body weight can be a practical way to obtain a good predictor for FF_{SW} more in line with how the traits most likely should be defined in the breeding objective. However, adjusting a trait for another genetically correlated breeding objective trait may affect the genetic and residual variances of the adjusted trait and its genetic and residual correlation to other traits. Only if the adjusted trait and the correlated trait have equal heritability and equal genetic and residual correlation, the two traits are genetically independent. This has been shown for feed intake adjusted for a production trait, but apply to any other trait that is defined as a linear function of another trait (Kennedy et al., 1993). To what degree FF_{SA} will be adjusted also for its genetic relationship to GR_{SA} is therefore dependent of the magnitude of both the genetic and residual (co)variances of the traits, and consequently in most cases with an unknown and maybe also non-wanted effect on the relative genetic gain of the traits.

The pre-correction of FF_{SA} also revealed that $preFF_{SA}$ is a trait more similar to FF_{SW} as inferred from the much higher genetic correlation between preFF_{SA} and FF_{SW} (0.81) than between FF_{SA} and FF_{SW} (0.45). This indicates that the purpose of recording quality traits at *SW* rather than at *SA* is mainly to obtain reliable genetic correlations that are more in line with their most likely definition in the breeding objective.

How to perform a simultaneous selection for increased growth rate and reduced body fat is also an important issue in livestock species. However, literature addressing how to treat high unfavorable genetic correlations between traits is limited. High genetic correlations have been detected between body weight and intramuscular fat when the traits were measured at the same age; e.g., 0.71–0.84 in broilers (Zerehdaran et al., 2004) and 0.87 in Texel sheep (Clelland et al., 2014). In fattening pigs a high genetic correlation is also found between growth rate and carcass fat growth, both measured from 25 to 100 kg live weight, and thus slaughtered at about the same body weight (0.84 in Landrace, 0.72 in Duroc), while the genetic correlation between growth rate and muscle (lean) growth during the same period was close to zero (−0.06 in Landrace, 0.07 in Duroc) (Gjerlaug-Enger et al., 2012). Based on the findings in this study, an alternative for terrestrial animals species could be to measure the carcass quality traits at about the same body weight and thus over a period of time. Then apply Gibbs threshold model to correct the body weight records for the selection performed for growth rate at the time of recording the quality traits and thus obtain predicted quality traits records less dependent on body size.

CONCLUSION

The estimated genetic correlations of growth rate with filet fat, filet pigment and visceral index were found to be sensitive to whether the traits were recorded at the same age or about the same body weight. In commercial production, increased genetic growth potential is expected to be realized through reduced production time and thus slaughtering the fish at a younger age. Hence, genetic correlations between growth rate and carcass quality traits recorded at about the same body weight are likely more relevant than those recorded at the same age. The result indicates that selection for increased growth rate is not expected to have a detrimental effect on the studied carcass quality traits given that the increased growth potential is realized through a reduced production time.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because On request authorities on Iceland stated that obtaining body weights on live fish does not require a special permit. The other traits were recorded on dead fish. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

BG and JØ designed the study. ÓK, BG, ML, and JØ carried out the statistical analysis and interpreted and discussed the results. ÓK conducted the experiments and wrote a first draft of the manuscript in close cooperation with BG and ML. BG, ML,

and JØ reviewed and approved the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: ÓK was employed by the company Stofnfiskur HF.

The remaining authors where employed by the offical reaserach institude Nofima. Stofnfiskur pays for the supervision of ÓK at Nofima, but the remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX

APPENDIX 1 | Summary statistics of available prediction models for filet fat and filet pigment, using NIR (Near Infrared) and VIS (Visual) reflectance spectroscopy measures andby means of PLS (partial least squares) orCPLS (canonical partial least squares) regression.

Model developer	Dependent variable	Type of tissue	No. of records	Prediction model method	RMSEP	R^2
Segtnan et al. (2009)	Filet fat	Plugs	145	PLS	1.96%-units	0.90
Kristjánsson (2012)	Filet fat	Plugs	120	PLS	2.02%-units	0.88
Kristjánsson (2012)	Filet fat	Plugs	120	CPLS	1.88%-units	0.90
Kristjánsson (2012)	Filet fat	Whole filet	24	CPLS	0.39%-units	0.99
Kristjánsson (2012)	Filetpigment	Whole filet	24	PLS	0.84 mg/kg	0.82

RMSEPis the Root Mean SquaredError of Prediction) and R^2 is the coefficient of determination of the model.

APPENDIX 2 | Estimates of published genetic correlations of growth rate (GR) with filet fat (FF), filet pigment (FP) and visceral fat (VF), and of FF with FP and VF; when these traits were all measured at the same age (SA) in several farmed fish species.

$r_{GR,FF}$	$r_{GR,FP}$	$r_{GR,VF}$	$r_{FF,FP}$	$r_{FF,VF}$	Species	References
0.42	0.31	−0.64	−0.82	−0.67	Atlantic salmon	Rye and Gjerde (1996)
0.45	0.2		0.00		Atlantic salmon	Vieira et al. (2007)
0.34–0.75	−0.41–−0.19		−0.3		Atlantic salmon	Powell et al. (2008)
0.84	−0.17		−0.19		Atlantic salmon	Tsai et al. (2015)
−0.19	0.21	0.19	−0.44	−0.33	Rainbow trout	Gjerde and Schaeffer (1989)
−0.12	0.36	0.38	0.13	−0.43	Rainbow trout	Kause et al. (2002)
0.24–0.36	0.50–0.73		−0.67–0.02		Coho salmon	Iwamoto et al. (1990)
0.73					Coho salmon	Neira et al. (2004)
	0.15–0.25				Coho salmon	Dufflocq et al. (2017)
0.82	0.65		0.22	0.91	Arctic charr	Elvingson and Nilsson (1994)
0.59	−0.61				Arctic charr	Wolters et al. (2013)
0.59					Common carb	Kocour et al. (2007)
−0.08			0.55		European white fish	Kause et al. (2011)
0.29					Sea bream	García-Celdrán et al. (2015)
0.59	−0.33	−0.13	−0.37	−0.12	Atlantic salmon	Current study

Paper 2

Stochastic simulation to evaluate the sensitivity of (co)variance estimates from a longitudinal Bayesian model for the left-censored Gaussian trait growth rate and the correlated trait fillet fat in Atlantic salmon.

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Abstract

In this study, we investigated to what extent a Bayesian multivariate model for the left-censored Gaussian trait growth rate implemented through a Gibbs sampler procedure managed to account for the selection in the data introduced when practising repeated harvesting of only the largest fish at different slaughter events. This was obtained through a stochastic simulation study where the genetic (co)variances among the two studied traits were obtained from a group of Atlantic salmon slaughtered at the same age (SA), for which the genetic correlation between growth rate and fillet fat was 0.59. First, we generated growth rate and fillet fat records of 2000 fish at each day of a 420 days growth period (2 to 12.3 kg and with five different regression coefficients (slope) ($\beta_{11} = 0.000$, $\beta_{12} = 0.009$, $\beta_{13} = 0.018$, $\beta_{14} = 0.027$, $\beta_{15} = 0.036$ %-units increase in fillet fat per day) of the fillet fat on the age (body weight) of the fish. Then we obtained data from the simulated dataset, which mimics repeated harvesting and recording of the body weight and fillet fat of only the largest fish at different slaughter group scenarios with a different number of slaughter events ($n = 1, 2, 4, 6, 8, 10, 20, 30$ or $C =$ when each fish passed 4.4 kg). For fillet fat, the true breeding values for each fish was defined as fillet fat at 4.4 kg and thus in line with the most likely defined breeding objective of this trait. The estimated breeding values for fillet fat was biased upwards and increased with an increase in the slope of the fat curve or increased number of slaughter events but of relatively modest magnitude expressed as a percentage of the overall mean filet fat (3.8 % to 10.3 %) of the fish for the different fat curves. The accuracy of selection for the estimated breeding values for fillet fat was for all scenarios in range of 0.62-0.83. The magnitude of the genetic correlation between growth rate and fillet fat was sensitive to the magnitude of the slope of the fillet fat curve slope. For the simulated six slaughter event case ($n = 6$), the estimated genetic correlation was 0.53, -0,01, -0.46, -0.70 and -0.81 for slope $\beta_{11}, \beta_{12}, \beta_{13}, \beta_{14}$ and β_{15}, respectively. It was concluded that the appropriate number of slaughter events was six or more to obtain close to unbiased parameter estimates for the total number of fish simulated in this study where a constant rearing environment was assumed and that the growth rate and fillet fat records obtained from the proposed repeated slaughter event scenario and analysed with the applied Bayesian model can be used to obtain genetic parameters for traits at similar body weight.

Introduction

In fish selective breeding programs, the growth rate is recorded when the actual population(s) have attained the desired average body weight. All fish are slaughtered over a few days and thus at about the same age. In some breeding programs, additional carcass quality traits are recorded at the same time. In a recent study in Atlantic salmon growth rate (g/day), fillet fat (%), fillet pigment (mg carotenoids/kg) and visceral (fat) index (weight of viscera/body weight) were recorded on two groups of animals from the same families; one of the group at the same age (*SA*) of the fish and the other group at about the same body weight (*SW*) through slaughtering the largest fish at five slaughter events and the remaining fish at the sixth slaughter event over six months (Kristjansson et al., 2020). The genetic correlation between the same trait in the two groups was high for growth rate (0.91 ± 0.05) and visceral index (0.86 ± 0.05), medium for fillet fat (0.45 ± 0.17) and low for fillet pigment (0.13 ± 0.27). Within each of the two *SA* and *SW* groups, the genetic correlation between growth rate and fillet fat changed from positive (0.59 ± 0.14) in the *SA* group to negative (-0.45 ± 0.17) in the *SW* group. An opposite change was seen for the genetic correlation between growth rate and fillet pigment that changed from negative (-0.33 ± 0.22) in the *SA* group to positive (0.62 ± 0.16) in the *SW* group, while that between growth rate and visceral index changed from slightly negative (-0.13 ± 0.16) in the *SA* group to slightly positive (0.19 ± 0.17) in the *SW* group. The genetic correlation between the traits within the *SA* group was in agreement with estimates from other studies in Atlantic salmon as well as studies in other farmed fish species where the two traits were recorded at the same age of the animals (see estimates and references in Appendix 2 in Kristjansson et al. (2020)). No published estimates are found to authors knowledge for similar traits recorded at about the same body weight, neither for any fish nor terrestrial animal species.

The genetic correlations of growth rate with carcass quality traits seem, therefore, to be sensitive to whether the latter traits are measured at the same age or the same body weight. Recording growth rate and the mentioned carcass quality traits at about the same body weight, rather than at the same age, was done based on the assumption that the genetic gain in growth rate is capitalised through the slaughter of similar sized fish at a younger age. Hence, measuring carcass quality trait at the market size of the individual fish, rather than at average market size, is more in accordance with how the traits should be defined in the breeding objective.

The parameter estimates mentioned above from Kristjansson et al. (2020) were obtained from a longitudinal Bayesian multivariate model previously developed for truncated binomial traits (Ødegård et al., 2010) using Gibbs sampler. The truncation model was also implemented for the Gaussian trait, as shown in Kristjansson et al. 2020. The model is implemented in DMU (Jensen et al., 2014). The growth rate and the carcass trait records were obtained from the largest fish slaughtered at the five first slaughter events and for all the remaining fish at the sixth slaughter events, while imputed growth rate records using the Gibbs sampler were obtained for the not slaughtered and not recorded and thus left-censored *SW* group fish at the first five slaughter events.

The mean observed and estimated growth rate at each of the six slaughter events (Figure 2 in Kristjansson et al., 2020) showed that the Bayesian multivariate model estimated increased growth rate over the period (as expected from knowledge about salmon growth curves), despite the reduction over time for observed growth rate since the largest fish were slaughtered first. This indicated that the Bayesian multivariate model managed to account for the left censoring of the growth rate trait at the first five slaughter events.

Therefore, the main objective of this study was to evaluate to what extent the Bayesian bivariate model manages to account for the left-censored growth rate trait and thus produce unbiased genetic parameters for both the carcass traits and growth rate in Kristjansson et al. (2020). This was obtained through a stochastic simulation study where the genetic (co)variances among the traits are assumed to be known as well as the development of the trait by increasing age. The study was limited to a bivariate model with growth rate and fillet fat only. Included was also a study of the effect of performing a different number of slaughter events on the unbiasedness of the genetic parameters and the impact of a various increase of fillet fat by age on the quantitative parameters.

Material and methods

The assumed family structure and input parameters are from the SA group in Kristjansson et al. (2020), for which the studied traits (growth rate, fillet fat, fillet colour and visceral (fat) index) were recorded on fish of the same age. For growth rate, the segmentation of the phenotype into additive genetic, repeatability and residual effects is from the SW group for which the same traits were recorded on fish of about the same body weight (BW). In this stochastic simulation study of growth rate gr/day (GR) and fillet fat % (FF), the genetic and permanent environment correlations between the same trait at different days (ages) was assumed to be unity, while the residual correlation was assumed to be zero. Genetic and residual variances were assumed to be unity within each day when being simulated and thereafter scaled according to an assumed growth curve and different fat curves along with a fixed coefficient of variation (CV) for each of the two traits within each time point. By this design, the estimated parameters within any day are similar to those obtained in the SA group in the real dataset, the heritability of both traits was constant over time, and by performing six simulated slaughter events, the estimated parameters obtained are similar to those obtained in the SW group in the real dataset.

True breeding values

The base population (generation 0) consisted of 150 animals (50 sires and 100 dams with a true breeding value (TBV) drawn from a multivariate normal distribution using the statistical program R (R Development Core Team, 2018) with the MASS (Venables and Ripley, 2002) package. TBV of the animals for traits BW and FF in generation $t = 0$ was calculated as:

$$\boldsymbol{TBV}_{\boldsymbol{t=0}\,\boldsymbol{(FF,BW)}} = \boldsymbol{N}_{\boldsymbol{t=0}}(\boldsymbol{0}, \boldsymbol{a}) \quad \text{with} \quad \boldsymbol{a}_{\boldsymbol{(FF,BW)}} \sim \begin{bmatrix} \boldsymbol{1} & \boldsymbol{0.58} \\ \boldsymbol{0.58} & \boldsymbol{1} \end{bmatrix} \qquad (1)$$

where $\boldsymbol{a}$ is the additive genetic (co)variance matrix between BW and FF recorded on fish at the same age. A nested mating design among the 150 randomly selected base population animals (one sire mated to two different dams and each dam to one sire only) was used to generate 100 full-sib families in generation 1.

The TBV of the animals in generation $t = 1$ and $t = 2$ was the average of their parent $TBV_{t-1(FF,BW)}$ plus the Mendelian sampling term, drawn from a multivariate normal distribution ($\boldsymbol{N}$):

$$\boldsymbol{TBV}_{\boldsymbol{t}\,\boldsymbol{(FF,BW)}} = \boldsymbol{0.5}\,\boldsymbol{TBV}_{\boldsymbol{t-1}\,\boldsymbol{(FF,BW)}\ \boldsymbol{sire}} + \boldsymbol{0.5}\,\boldsymbol{TBV}_{\boldsymbol{t-1}\,\boldsymbol{(FF,BW)}\,\boldsymbol{dam}} + \boldsymbol{N}_{\boldsymbol{t(FF,BW)}}(\boldsymbol{0}, \boldsymbol{0.5a}) \qquad (2)$$

The generation 2 animals were the offspring of 50 sires and 100 dam parents randomly selected from the generation 1 animals such that the offspring of each of the selected sires had a different grandsire parent and the offspring of each of the selected dams had a different granddam parent. Related sire and dam parents (half-sibs) were not mated. For each mating, 20 individuals were generated with a $TBVt_{t(FF,BW)}$, resulting in a dataset of 2000 individuals. The variance of $TBV_{t(FF,BW)}$ was unity in all

simulated generations ($t = 0, 1, 2$), thus maintaining the genetic covariance (correlation) of 0.58 in all generations.

The residuals

The simulated animal traits FF and BW had one record for each trait per day j for 421 ($j = 0, 1, \ldots, 420$) consecutive days (60 weeks). Within each day, the residual variation of FF and BW was unity, and their residual covariance and correlation 0.69. Between the different days, the residual covariance (correlation) was zero. Thus, the residual (co)variance matrix was:

$$\boldsymbol{e} = \begin{bmatrix} \boldsymbol{s_0} & \cdots & \boldsymbol{0} \\ \vdots & \ddots & \vdots \\ \boldsymbol{0} & \cdots & \boldsymbol{s_{420}} \end{bmatrix}$$

where $\boldsymbol{e}$ is of dimension 842 × 842 since there were 421 days and two traits, and the residual (co)variance matrix within each day ($\boldsymbol{s_j}$):

$$\boldsymbol{s_j} \sim \boldsymbol{N}\left(\boldsymbol{0}, \begin{bmatrix} \boldsymbol{1} & \boldsymbol{0.69} \\ \boldsymbol{0.69} & \boldsymbol{1} \end{bmatrix}\right) \qquad (3)$$

The mean phenotypes at each day

Body weight

A growth curve was needed to generate the 2000 individual phenotypes for FF and BW at each of the 421 days. This was obtained by assuming that the mean body weight ($\overline{BW_j}$) at each time point ($j = 0, \ldots, 420$) followed a growth curve, defined by the formula for the thermal growth coefficient (TGC) (Jobling, 2003) where the water temperature was 10°C (t) over the entire growth period, the start BW was 2 kg (BW_0 at day $j = 0$) and TGC was 2.5, and the mean body weight at date j was:

$$\overline{\boldsymbol{BW_j}} = \left\{\left(\sqrt[3]{\boldsymbol{BW_0}} + [(\boldsymbol{TGC/1000}) \times (\boldsymbol{j} \times \boldsymbol{t})]\right)\right\}^{\boldsymbol{3}} \qquad (4)$$

resulting in $\overline{\boldsymbol{BW}}_{\boldsymbol{420}} = 12.3$ kg on the last day.

Fillet fat

The increase in mean FF over the 421 days growth period was assumed to be linear:

$$\overline{\boldsymbol{FF}}_{\boldsymbol{mj}} = \boldsymbol{\beta_0} + \boldsymbol{\beta_{1m}}\mathbf{j} \qquad (5)$$

where the intercept was assumed to be $\beta_0 = 10$; i.e., on average, 10 % FF at $j = 0$ at which the fish were assumed to be on average 2 kg. The FF curve had five different slopes ($m = 1, \ldots, 5$) with the same intercept of 10 % fat at day $j = 0$. The chosen slope for $m = 3$ ($\beta_{13} = 0.018\ \% - units/day$) gave the same parameter estimates as for the SA group in the real data. The slope for $m = 2$, $m = 4$ and $m = 5$ was 0.5 ($\beta_{12} = 0.009\ \% - units/day$) 1.5 ($\beta_{14} = 0.027\ \% - units/day$) and 2.0 ($\beta_{15} = 0.036\ \% - units/day$) times larger than that for $m = 3$; while that for $m = 1$ was set equal to zero ($\beta_{11} = 0.000\ \% - units/day$) thus resulting in a mean FF of 10 % at all days ($j = 0, 1, \ldots, 420$). For the four other fat curves, the mean FF value of the population at day $j = 420$ was $\overline{FF}_{2,420} = 13.8\%$, $\overline{FF}_{2,420} = 17.6\%$, $\overline{FF}_{4,420} = 21.4\%$ and $\overline{FF}_{5,420} = 25.2\%$.

Scaling of the variances

For BW the assumed heritability was $\boldsymbol{h_B^2} = 0.40$, the repeatability $\boldsymbol{r_B^2} = 0.40$, and the residual $\boldsymbol{e_B^2} = 0.2$, all expressed as a proportion of the sum of the additive genetic, repeatability and the residual

variances. For FF the assumed heritability was $\boldsymbol{h_F^2} = 0.25$ and $\boldsymbol{e_B^2} = 0.75$, expressed as a proportion of the sum of the additive genetic and residual variances.

The phenotypic coefficient of variation (CV) of BW ($\boldsymbol{CV_{pBW}}$=0.27) and FF ($\boldsymbol{CV_{pFF}} = 0.10$), both estimates obtained from the SA group in Kristjansson et al. (2020), was assumed to be constant over the 421 days growth period.

The coefficient of variation of the additive genetic ($\boldsymbol{CV_a}$), the repeatability ($\boldsymbol{CV_r}$) and the residual ($\boldsymbol{CV_e}$) part of the phenotypic coefficient of variation was obtained as:

$$\boldsymbol{CV_a} = \sqrt{\boldsymbol{h^2}} \times \boldsymbol{CV_p} \qquad (6)$$

$$\boldsymbol{CV_r} = \sqrt{\boldsymbol{r^2}} \times \boldsymbol{CV_p} \qquad (7)$$

$$\boldsymbol{CV_e} = \sqrt{\boldsymbol{e^2}} \times \boldsymbol{CV_p} \qquad (8)$$

The phenotype

When adding all previously described parts for animal i at day j, the phenotype becomes

$$\boldsymbol{P_{BWij}} = \overline{\boldsymbol{BW}}_j + \boldsymbol{CV_{aBW}}\overline{\boldsymbol{BW}}_j\boldsymbol{TBV_{t=2\,(BW)i}} + \boldsymbol{CV_{rBW}}\overline{\boldsymbol{BW}}_j\boldsymbol{N(0,r)_i} + \boldsymbol{CV_{eBW}}\overline{\boldsymbol{BW}}_j\boldsymbol{N(0,e)_{BWij}} \quad (9)$$

The trait GR for each fish was obtained by dividing the phenotype of BW by the age of the fish, which ranged from 500 to 921 days ($j = 0, \ldots, 420$) since the fish was assumed to be 500 days old at 2 kg BW.

For FF the phenotype (P_{FFijm}) for animal i at time point j, with curve m, was generated as follows:

$$\boldsymbol{P_{FFijm}} = \overline{\boldsymbol{FF}}_{jm} + \boldsymbol{CV_{aFF}}\overline{\boldsymbol{FF}}_{jm}\boldsymbol{TBV_{t=2\,(FF)}} + \boldsymbol{CV_{eFF}}\overline{\boldsymbol{FF}}_{jm}\boldsymbol{N(0,e)_{FFij}} \qquad (10)$$

Figure 1 shows the development of the mean growth rate (GR) and the mean fillet fat (FF) over the 421 days growth period. The bars represent the standard deviation of the traits at some of the days.

Slaughter algorithm

All fish received a GR record when the mean weight of the population reached 2.7 kg ($j = 50$), which was the mean body weight of the SW fish in the real data when placed in the experimental tanks. The following simulated slaughtering algorithm was conducted, which divided the population of animals ($N = 2000$) into $n \in (1, 2, 4, 6, 8, 10, 20, 30, \mathrm{C})$ different slaughter group scenarios. Slaughter event took place when $1/n$ of the largest fish of the remaining part of the population passed 4.4 kg. Thus for $n = 1$, all fish were slaughtered when the mean body weight of the population passed 4.4 kg; for $n = 2$ approximately 50 % (depending on the values retained from the normal distributions) of the population was slaughtered when the mean body weight of this proportion of the largest fish in the entire population passed 4.4 kg; while $n = C$ (continuous) is the number of slaughter groups needed for each fish to pass 4.4 kg before being slaughtered, which could result in only one or a few fish being slaughtered at each slaughter event. For all groups (except $n = 1$ and $n = C$) the final slaughter event was set four weeks after the second last slaughter event, or when the proportion of the remaining slow-growing fish was less than $1/n$ and would not pass the set threshold value of 4.4 kg within the 421 days simulated growth period. This procedure corresponds to that used in Kristjansson et al. (2020), where the slaughter took place over six slaughter events ($n = 6$), and where all the remaining

fish were slaughtered at the sixth slaughter event, which took place 29 (year-class 1) and 34 (year-class 2) days after the 5th slaughter event.

Each slaughtered fish received a growth rate record and a fillet fat record at each slaughter event, while each of the not slaughtered fish still alive received a phantom growth rate record from the Gibbs sampler in the Bayes model in the parameter estimation where the upper bound of the Gibbs sampling was defined by the growth rate of the smallest sampled fish at each sampling.

Statistical model

The model applied for parameter estimation was a longitudinal Bayesian model for left-censored Binomial trait using the DMU software (Ødegård et al., 2010) using the Gaussian alternative described in Kristjansson et al. 2020 for the following bivariate linear mixed animal model:

$$\boldsymbol{Y} = \begin{bmatrix} \boldsymbol{FF} \\ \boldsymbol{GR} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X\beta + Zu + e} \\ \boldsymbol{X\beta + Zu + Mr + e} \end{bmatrix} \qquad (11)$$

$\boldsymbol{Y}$ vector of the two simulated traits FF and GR obtained using the slaughter algorithm where the animals still alive but not recorded received their threshold value for growth rate, which defined the threshold for the Gibbs sampler.

$\boldsymbol{\beta}$ vector of the fixed effect of slaughter event nr. for GR and only the overall mean for FF, and for which the estimates are BLUE (Best Linear Unbiased Estimate). For continuous sampling ($n = C$), only the overall mean for both GR and FF where included.

$\boldsymbol{u}$ vector of random animal additive genetic effects, $\boldsymbol{u} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{A} \otimes \boldsymbol{G_0})$, where $\boldsymbol{A}$ is the additive genetic relationship matrix and $\boldsymbol{G_0}$ is the additive genetic (co)variance matrix.

$\boldsymbol{r}$ vector of random repeatability effects $\boldsymbol{r} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{I}\sigma_r^2)$ due to repeated records of GR on the same fish. The number of repeated records depends on the number of slaughter events, but each animal received GR record when the mean weight of the population was 2.7 kg and then a simulated record from the Gibbs sampler when the individual was alive at sampling but not sampled and then a GR record at slaughtering.

$\boldsymbol{e}$ vector of random residual effect $\boldsymbol{e} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{I} \otimes \boldsymbol{R_0})$, where $\boldsymbol{R_0}$ is the residual (co)variance matrix.

$\boldsymbol{X}, \boldsymbol{Z}, \boldsymbol{M}$ the appropriate incidence matrices that link the observations to their levels of fixed and random effects.

The length of the Monte Carlo Marco chain (MCMC) was 1.5 million samples. The first 1000 samples were removed from the chain (burn-in). Every 1000 value of the chain was retained(interleaving).

Each simulation scenario had 20 replicates and the results presented are the means and the standard deviations (standard error of the estimate) of the 20 replicates for each of the parameters.

The convergence of the MCMC chain was determined by Raftery and Lewis's test (Raftery and Lewis, 1992) using the Coda package (Plummer et al., 2018) in the statistical program R (R Development Core Team, 2018). All parameters converged within these convergence criteria.

Evaluation criteria for the simulated data

The bias and the accuracy of the estimated breeding values, averaged over the 20 replicates, were the two evaluation criteria. The bias was calculated as:

$$\boldsymbol{Bias} = \frac{\sum(\boldsymbol{TBV} - \boldsymbol{EBV})}{\boldsymbol{N}} \qquad (12)$$

where TBV is the true breeding value, and EBV is the estimated breeding value, and $N = 2000$ is the total number of simulated animals with growth rate and fillet fat records.

The accuracy of selection; i.e. the correlation between the true and estimated breeding value, was calculated as:

$$\boldsymbol{Accuracy} = \frac{\boldsymbol{cov(TBV, EBV)}}{\boldsymbol{sd(TBV)sd(EBV)}} \qquad (13)$$

where $sd(TBV)$ and $sd(EBV)$ is the standard deviation of the true and the estimated breeding value, respectively. The TBV for GR for animal i was

$$\boldsymbol{TBV_{GRi} = TBV_{t=2\,(BW)i}} \qquad \textbf{(14)}$$

were $TBV_{t\,(BW)i}$ is from equation 9, while the EBV_{GRi} were the solutions of the additive genetic effect from the animal model in equation 11.

The TBV of FF of each individual i was taken from the day j each individual first passed 4.4 kg as this definition is more in line with the defined breeding objective of the trait as discussed in Kristjansson et al. (2020); thus the TBV of FF was defined as:

$$\boldsymbol{TBV_{FFijm} = \overline{FF}_{jm} + CV_{aFF}\overline{FF}_{jm}TBV_{t=2\,(FF)}} \qquad \textbf{(15)}$$

The overall mean FF at each slaughter event (time point) was added to the TBV. The EBV of FF was the solution from the model in equation 11 using the phenotype defined in equation 10 and adding the fixed effect solution from the parameter estimation to the additive genetic effect estimates.

In addition to estimating the overall bias and accuracy, the bias and accuracy of the EBVs were calculated at each simulated slaughter event of the different slaughter group scenarios, at which the actual animals within the sampling group were picked out, and their accuracy and bias calculated.

Results

For the first eight different slaughter group scenarios ($n = 1, 2, 4, 6, 8, 10, 20$ and 30), the average number of fish slaughtered from the 20 replicates at the first slaughter event (and in parentheses the average day of 20 replicates the first slaughter event took place) was 2000 (day 550), and about 1016 (day 651), 515 (day 615), 345 (day 602), 264 (day 595), 210 (day 589), 108 (day 575) and 72 (day 568) respectively. For slaughter group scenarios $n = 20$, 18 of the 20 replicates terminated at the 19th simulated slaughter event since, at the18th slaughter event, less than 1/20 individuals were left. For the slaughter group scenarios $n = 30$, 15 of the 20 replicates terminated at the 28th samplings and the remaining 5 at the 29th slaughter event since less than 1/30 of the fish were left for the second last slaughter event.

For fat curve 3, the average fillet fat was about 12.9 % at day 658 (4.51 kg) (Figure 1). For the six-slaughter event case the average fillet fat of all the slaughtered fish was 13.4 %; i.e., 12.6 (345 fish), 13.0 (348 fish), 13.2 (345 fish), 13.6 (345 fish), 14.2 (388 fish) and 14.0 (280 fish) % at each of the six slaughter events across the 20 replicates.

Figure 2 shows that for each of the six shown slaughter group scenarios ($n = 8$ not shown as very similar results as for $n = 6$) the mean observed growth rate decreased over time as expected as the fastest-growing animals were slaughtered first, as opposed to the estimated growth rate that increased over the same period. The estimated (BLUE) growth rates followed the true simulated growth rates over the first ~2/3 of the slaughtering events, after which they were lower than the true growth rates.

Figure 3 shows that for the six ($n = 6$) and the continuous ($n = C$) slaughter event cases, the estimated heritability for growth rate and fillet fat for each of the five different fat curves were close to their input values. However, the estimated genetic correlations between the two traits changed from being positive and close to the input (within-day) value for fat curve 1 (no change in fillet with increasing body weight) to close to zero for fat curve 2 and to increasing negative values the more the filet fat increased with increasing body weight (fat curve 3, 4 and 5). For the six-slaughter event case, the residual correlation decreased marginally for the different fat curves. However, for the continuous slaughter event case, the residual correlation changed from positive but substantially lower than their input values for fat curve 1, while it for the other fat curves changed in the same direction as the genetic correlation but with a less magnitude.

Figure 4 shows that for both the six-slaughter event case and the continuous slaughter case, the accuracy of the estimated breeding values was stable at about 0.6-0.7 for both the traits and that the bias for growth rate was negligible for each of the five different fillet fat curves. However, for the six-slaughter event, the bias for fillet fat increased from being negligible for fat curve 1 (no change in fillet fat with increasing body weight) to a value of ~ -1.7 % units (and thus higher than their true values) for fat curve 5. For the continuous slaughter event case, the mean estimated breeding values for fillet fat were all higher than their true values, also for fat curve 1. For the six-slaughter event case, the estimated bias for fillet fat, as a percentage of the phenotypic mean value, was 3.8 % for fat curve 2, 6.4 % for fat curve 3, 8.6 % for fat curve 4 and 10.3 % for fat curve 5.

Figure 5 for fat curve 3 shows that the heritability estimates for both fillet fat and growth rate were similar to their input values, irrespective of the number of slaughter events. The estimated genetic correlation between fillet fat and growth rate decreased with an increasing number of slaughter events from its positive input value for slaughter group $n = 1$ until negative values from $n = 4$ onwards to $n = 30$. In contrast, the genetic correlation was slightly less negative for the continuous slaughter event case than for $n = 20$ and $n = 30$. The estimated residual correlations decreased from about 0.6, which is slightly lower than its positive input for $n = 1$ to about 0.30 for $n = 30$, but to a negative value of -0.23 for $n = C$.

Figure 6 for fat curve 3 shows that the accuracy of the estimated breeding values for growth rate was about 0.74-0.78 and similar for all the nine slaughter group scenarios. For fillet fat, accuracies of the same stable magnitude as for growth rate was found for slaughter scenarios $n = 6$ to $n = 30$, slightly lower accuracies for $n = 4$ and $n = C$, but with substantially reduced accuracy for $n = 1$ and $n = 2$. The bias of the estimated breeding values for growth rate was negligible for all nine slaughter group scenarios, while the bias for fillet fat increased (become larger than their true values) with an increasing number of slaughter events, and highest for $n = C$.

Figure 7 shows that for each of the eight slaughter group scenarios except for $n = 20$ and $n = 30$, the bias of the estimated breeding values for growth rate within slaughter event was negligible compared to their mean values (see Figure 1). For $n = 20$ particularly, but also for $n = 30$, the mean estimated breeding values were lower than their true values. For each slaughter group scenario, the accuracy of the estimated breeding values showed a decreasing trend with an increasing number of slaughter

events, except for the last slaughter event of $n = 1, 2, 4, 6$ and 8, at which the accuracy was higher than at the few previous events.

Figure 8 for fat curve 3 shows that for each of the eight slaughter group scenarios, the bias of the estimated breeding values for fillet fat was higher than the true values for all slaughter events and particularly so at the first than for the later slaughter events. For each slaughter groups scenario, the accuracy of the breeding values for fillet fat for the fish slaughtered at each slaughter event showed a decreasing trend over the first slaughter events and with an increasing trend over the following events.

Discussion

In this study, a proportion of the largest fish was assumed to be harvested and recorded at different numbers of subsequently slaughter events, thus introducing a confounding effect between the fish's growth rate and the slaughter event. This will result in biased genetic parameters for the trait growth rate and other correlated traits recorded on the slaughtered fish if not appropriately accounted for. The objective of this study was through stochastic simulation to evaluate to which extent a longitudinal Bayesian model, implemented through a Gibbs sampler procedure that assigned phantom growth rate phenotypes to the non-slaughtered fish at each slaughter event, managed to account for the systematic and directional harvesting of only the largest fish at the different slaughter events. The model's sensitivity to different slopes of the regression of fillet fat on the age (body weight) of the fish was also studied.

If the studied trait fillet fat could be recorded on live fish and all fish were recorded for both traits at each of the slaughter events, then no confounding effect between growth rate and recording event should be present. In that case, the repeated recorded SA data at all recording events could be analysed with an animal model with the recording event as a fixed effect with the number of levels equal to the number of recording events. Then the estimates of the levels of this fixed effect for each trait should be equal to the true mean growth rate and fillet fat in Figure 2. This data set would also give more information on the repeatability effect for growth rate (as well as for fillet fat) than that obtained from the six slaughter events of the SW group in the real data in Kristjansson (2020). Moreover, from a multivariate animal model where the trait at each recording event is treated as a separate trait, estimates of genetic and residual (co)variances for the traits could be obtained for the purpose of using more reliable input parameters for the present simulation study. Such a data set could also be used to evaluate the residual correlations obtained by the repeatability model since each individual receives a growth rate record from multiple timepoints while residual of fillet fat is estimated from a single timepoint. This difference is detected by the difference in residual correlation between $n =< 30$ and $n = C$ sampling events.

As obtaining reliable filet fat records require sacrificing the fish, and we want to obtain fat records on similar sized fish throughout their growth period, we are dependent on a statistical model to account for the directional selection in the growth data on the parameter (co)variance estimates of the two studied traits. In the simulation study, it was found that the fixed effect estimates for growth rate followed the true growth curve for most sampling events (Figure 2), meaning that the applied Bayesian model managed, through assigning phantom phenotypes to the non-recorded fish at each slaughter event, to account for the harvesting of the largest fish only at each slaughter event. However, at the last slaughter events of each slaughter group scenario, at which only the slow growers were still alive, the fixed effect estimates for growth rate were lower than the true estimates but higher than the recorded growth rate of the slaughtered fish at these slaughter events. This indicates that the statistical model did not fully compensate for the repeated slaughter event strategy. The reasons for this could be

few fish with growth records (counting both real and phantom records), particularly at the last slaughter events for the slaughter scenarios with a high number of slaughter events ($n = 20$ and $n = 30$, for which some replicates have very few or no fish left), and an insufficient correction for the fact that only the slowest growing fish are left in the tank at the last slaughter event.

Of great interest is the large effect of the fat curve on the estimates of the genetic correlation between growth rate and fillet fat. For no change in fillet fat with increasing body weight (fat curve 1), the genetic correlation was equal to the positive input correlation (0.58), while it decreased and to negative value the more the fillet fat increased with increasing body weight. A similar reduction in the residual correlation with increasing body fat, but with a lesser magnitude, was only seen for the continuous slaughter event case (Figure 3). Residual correlation between a trait with a single measurement and a trait modelled with a repeatability model should, however, be treated with caution, as it will not be clearly defined. The average fillet fat of about 15.3 % (17.0 %) for fat curve 4 (curve 5) at day 695 (5.31 kg) corresponds to that for farmed salmon in Norway with a fillet fat of 16.5 % (whole-body fat 21.5 %) when slaughtered at about 5.3 kg (Aas et al., 2019).

It can be shown that if body fat (%) increases with age (and body weight) and the fish are harvested at the same body weight, the phenotypic correlation between body fat and growth rate becomes negative. This is because as body fat on average increases with age, at the same body weight, the faster-growing individuals are younger and thus have lower body fat. The correlation can be altered down (up) by increasing (decreasing) the regression coefficient of body fat on age. In this study, the above was shown to be the case for the genetic correlation but not for the residual correlation. The phenotypic correlation can also be altered down (up) by increasing (decreasing) the growth rate of the fish and by decreasing (increasing) the coefficient of variation of body fat, thus making the effect of the given correlation on the increase of body fat with body weight (at fixed age) weaker so that the faster-growing fish being younger dominates.

The magnitude of the genetic and phenotypic correlation between body weights at different time points decreases from relatively high to medium values as the time between the recordings increases (Gjerde et al., 1994). The same pattern is also expected for fillet fat as deposition of fillet fat increases with age and is especially high during declining day length in autumn (Rørvik et al., 2018). However, in this study, the genetic correlation between the same trait on different days was assumed to be unity and the residual correlation to be zero. The repeatability effect added to the additive genetic effect of the simulated body weights in this study implies that the phenotypic correlation between body weights at different days are much higher (0.8) than without this effect (0.4), and thus at a magnitude reported by Gjerde et al. (1994) for body weights 3 to 6 months apart in time (0.83-0.95). For fillet fat, the authors are not aware of any estimates of neither the genetic, the phenotypic, nor the residual correlation between fillet fat recorded at different ages or body weights. Consequently, the simulated dataset probably has a lower phenotypic and much lower residual correlation between different days than in real data.

The ability of the applied Bayesian model to produce accurate and unbiased estimates of genetic parameters was shown to be good for all the tested fat curves. Heritability for both traits and genetic correlation between the two traits were accurately estimated, irrespective of how FF varied over time. However, the negative bias of the $EBVs$ for FF (larger than the true values) increased with an increasing rate of fillet fat deposition by age (body weight) of the fish, but of a modest magnitude (4-10 %) as compared to the mean fillet fat values for each of the five FF curves. That is because the TBVs includes the value from the fillet fat curve at the day when the fish is 4.4 kg along with the scaled genetic value at that date by the $\boldsymbol{CV_{aFF}}$ for all the evaluated scenarios. While the $EBVs$ for FF

include the BLUE of the overall mean of FF across all timepoints. Thus, when the slope of the FF curve increases, the difference between samplings increases while the BLUE is fitted across all those sampling points as also seen when bias is evaluated within time points, the first sampled animals will be further bellow the BLUE estimate than later animals where the FF has increased with age (body weight). When the number of samplings is increased, the variation in observed FF increases since first samplings occur earlier and latest samplings occur later, which results in more difference in FF value among the dataset, which results in more bias since the BLUE for the EBV is fitted through all the time points.

The accuracy of selection for fillet fat (and growth rate) was similar for the different slaughter group scenarios and fat curves, implying that the same animals will be selected as parents for a new generation, but due to the observed bias for FF, the magnitude of the genetic gain for FF will be overestimated.

For all slaughter group scenarios except $n = C$, and for all fat curves, it was found that the estimated heritability of growth rate and fillet fat and their residual correlations were quite similar to their input values. In contrast, the estimates of the genetic correlations between the traits were largely affected by the increases in fillet fat by age (or body weight). For the case of the six-slaughter event with the intermediate FF curve 3, the estimated genetic correlations were negative and thus substantially lower than the positive genetic correlation in the SA group and close to the estimated genetic correlation between the traits obtained for the SW group (slaughtered at about the same body weight) in Kristjansson et al. (2020) in which about 1300 fish from each of two different year-classes were slaughtered over six slaughter events. For the higher number of slaughter event cases $n = 10$, 20, and 30), the genetic correlation was slightly lower than that for $n = 6, 8$ and C. This indicates that six or more slaughter events are the appropriate number of slaughter events for the total number of fish simulated in this study in which a constant rearing environment was assumed. This is also supported by the higher accuracy of the estimated breeding values for FF for these numbers of slaughter events as compared to a lower or higher number. In a practical situation where the rearing environment (e.g., water temperature, light day, fish density, feed composition and quality) may change over time, the estimated parameters and breeding values may become more biased as the Bayesian model may become less efficient in separating the genetic and environmental effect. Most probably, this will be the case when the fish are reared in floating net-cages in the sea where the different slaughter events have to take place over varying seawater temperature and light conditions from, e.g., March to September, thus introducing more environmental noise than, e.g., when such data were recorded under relative much more stable environmental conditions in tanks onshore in the experiments reported by Kristjansson et al. (2020).

When keeping the total number of animals slaughtered constant at each slaughter event, the number of animals slaughtered at each slaughter event will decrease with increasing the number of slaughter events. Hence, an optimal number of slaughter events is expected to depend on the total number of animals to be slaughtered. For a larger total number of animals slaughtered than in the simulation study, the optimal number of slaughter events is expected to be six or more without compromising the number of animals slaughtered per event. However, if repeated slaughter events have to be performed in practice to obtain unbiased genetic parameters, the number of slaughter events should be kept as low as possible to keep labour and facility cost as low as possible.

Conclusion

This stochastic simulation study shows that the applied longitudinal bivariate Bayesian model for the truncated left-censored Gaussian trait growth rate implemented through the Gibbs sampler for a given total number of animals can provide close to unbiased (co)variance estimates also for the correlated trait fillet fat if the number of subsequently slaughter events are sufficiently high and not too many. It was found if nr. of animals is 2000, an optimal number of sampling is six or more samplings to access fillet fat measured on same sized individuals. Therefore, this model can be used when the aim is to obtain genetic parameters for traits at similar body weight without repeat measuring of all the animals at several samplings. These results should also be of interest for traits correlated to the growth rate in other aquatic and terrestrial farm animal species and for which the breeding objective is defined as the trait value at the same body weight rather than at the same age.

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Figures

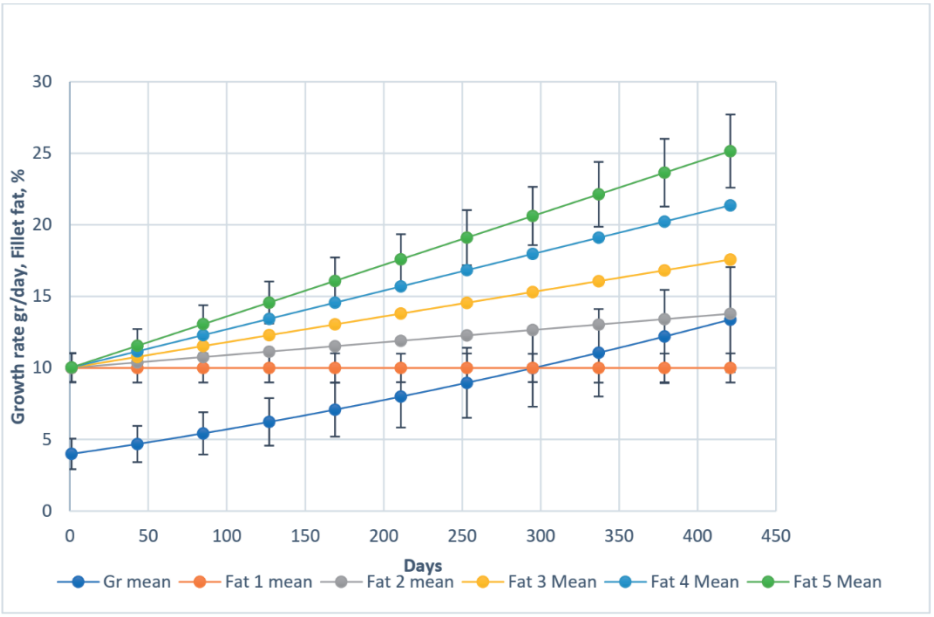


Figure 1. Development of the growth rate (blue line) and of the mean fillet fat for the five different fat curves over the 421 days growth period. The bars at some of the time points represent the standard deviations of the traits.

488

489 Figure 2. The mean observed growth rate (orange line) of the slaughtered fish at each slaughter event and the estimated
490 (BLUE) mean growth rate (blue line) of all fish (phantom and slaughtered) at each slaughter event. The true growth curve
491 (yellow line) is the value obtained from the formula for the thermal growth coefficient (for TGC=2.5) at each slaughter event.

492

493 Figure 3. Estimates (means and standard deviations of 20 replicates) of the given parameters for the five studied fat curves
494 for the six slaughter events (upper) and the continuous slaughter (lower) case.

Figure 4. Estimates of bias and accuracy of the estimated breeding values (means and standard deviations of 20 replicates) for the five studied fat curves for six slaughter events (upper) and continuous slaughter (lower).

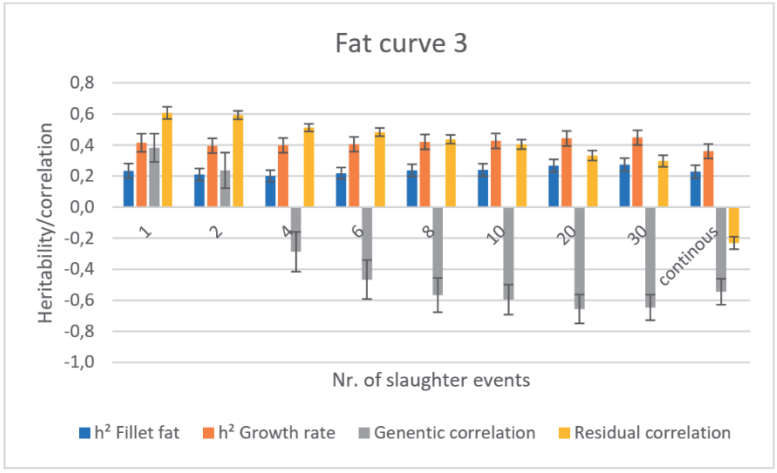
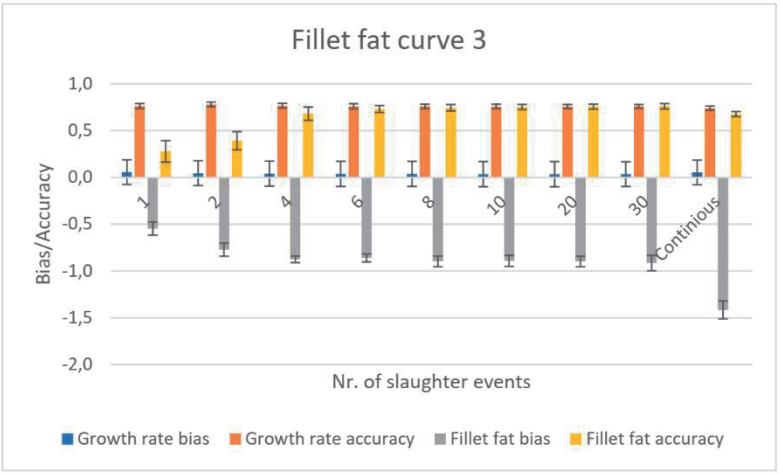


Figure 5. Estimates of heritability and genetic and residual correlations (means and standard deviations of 20 replicates) for fillet fat and growth rate for the 9 different slaughter group scenarios: all fish slaughtered having one fillet fat record, and two

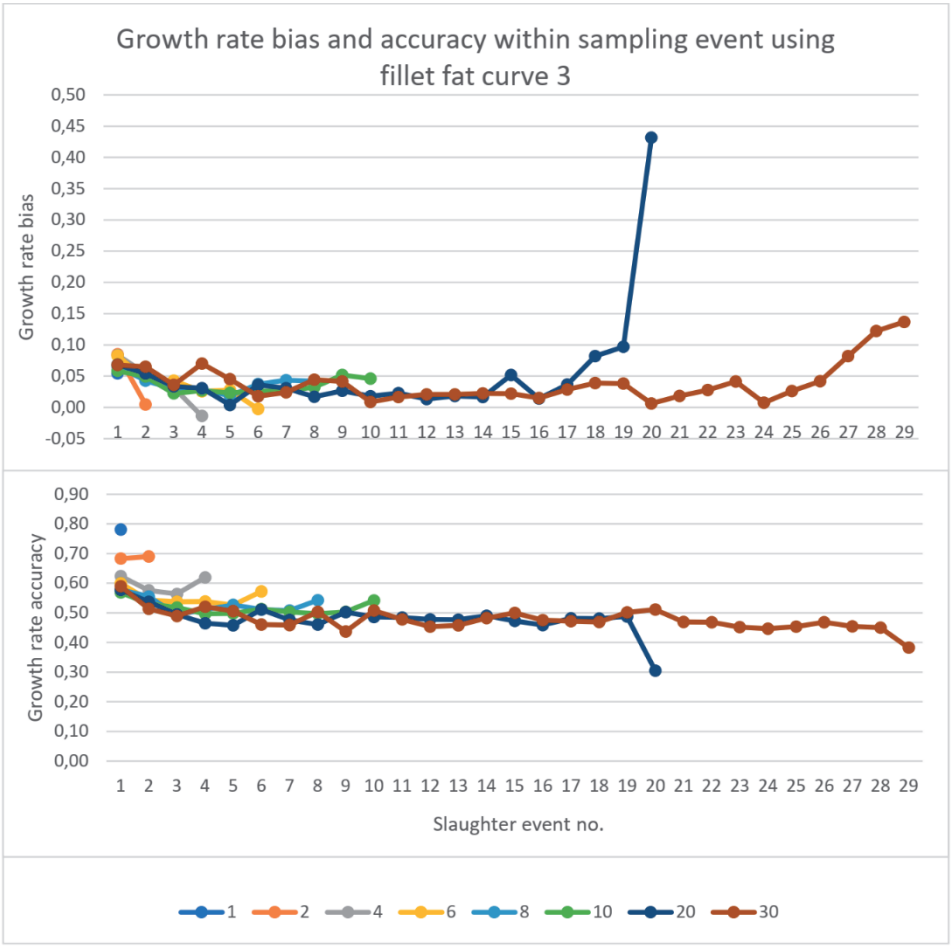
502 growth rate records (n=1); a decreasing number of fish slaughtered per slaughtering event (n=2, .., 30); and none, one or few
503 fish slaughtered per day (Continuous).

504



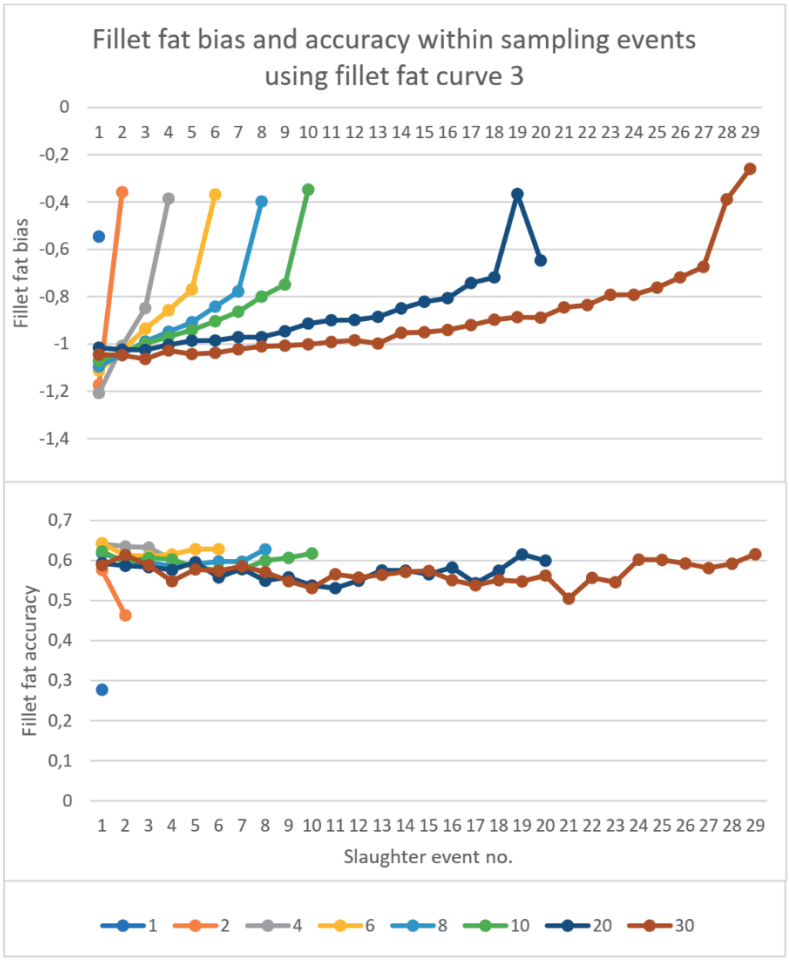
505

506 Figure 6. Estimates of bias and accuracy of the estimated breeding values (means and standard deviations of 20 replicates) for
507 fille fat and growth rate for the 9 different slaughter group scenarios, all with fat curve 3: one fillet fat record and two growth
508 rate records (n=1); or for a decreasing number of fish slaughtered per slaughtering event (n=2, …, 30); and none, one or a
509 few fish slaughtered per day (Continuous).



510

511 Figure 7. Estimates of the bias and the accuracy of selection (means and standard deviations of 20 replicates) of the
512 estimated breeding values for growth rate for the animals slaughtered at each slaughter event, for each of the eight slaughter
513 groups scenarios, each with fat curve 3. (Bias for n=1 is 0.05)



514

515 Figure 8. Estimates of the bias and the accuracy of selection (means and standard deviations of 20 replicates) of the estimated
516 breeding values for fillet fat for the animals slaughtered at each slaughter event, for each of the eight slaughter groups
517 scenarios all with fillet fat curve 3.

Paper 3

On adjustment of fillet fat for body weight when the traits are recorded on Atlantic salmon at the same age

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Abstract

Recording carcass quality traits at the same body weight rather than at the same age is more in line with how quality traits should be defined in the breeding objective. However, a common procedure is to measure body weight (***BW***) and fillet fat (***FF***) at the target average market size when the population of animals is at the same age. Since there is a relatively high positive genetic correlation between ***FF*** and ***BW*** is common to adjust the impact of ***BW*** on ***FF*** by including ***BW*** as a covariate in the statistical model or pre-adjust ***FF*** for ***BW*** before the parameter and breeding value estimation. By adjusting ***FF*** for the genetically correlated trait (***BW***) genetic variation in ***FF*** is reduced and may result in biased estimated breeding values and reduced genetic gain. The objective was to investigate how to obtain genetic parameters and breeding values for traits recorded on fish slaughtered at the same age that is comparable to those obtained when slaughtering the fish at the same ***BW***. This was investigated through a stochastic simulation study where the input (co)variances of the animals traits recorded at the same age (SA) and generated at each day of a 420 days growth period (2 to 12 kg). The true breeding values for ***FF*** was defined as ***FF*** at 4.4 kg. Estimates of (co)variances for ***BW*** and ***FF*** and breeding values were obtained from a bivariate animal model where four different methods were used to adjusted ***FF*** for ***BW*** (in addition to no adjustment); pre- or covariate adjustment for ***BW*** and pre-or covariate adjustment for residual of ***BW***. Estimates of expected genetic gain were obtained by selecting on an overall breeding value where the economic weight for ***BW*** was set equal to unity while those for ***FF*** was either -4, -3, -2, -1, 0, +1, +2, +3, +4. It was found that if the breeding goal is to reduce fillet fat and increase growth rate, adjusting ***FF*** for ***BW*** give a higher genetic gain in growth rate and a minor reduction in fillet fat as compared to performing no adjustment of the ***FF*** records. However, if the breeding goal is to increase both traits, no adjustment of ***FF*** for ***BW*** should be performed. This was also the conclusions when applying the same adjustment methods on a real data set.

Introduction

Growth rate and carcass quality trait (e.g., fillet fat and colour) are important production traits in farmed Atlantic salmon. Through selection for increased growth rate, fish reach the desired market weight at an earlier age. In selective breeding programs, the recording of growth and quality traits take place when fish of the same age have reached the desired average market body weight, at which there is a large variation in body weight among the fish. In a recent study, one group of fish slaughtered at the same age (SA) and a group of their sibs at about the same body weight (SW) at six different slaughter events (Kristjánsson et al., 2020). The genetic correlation between the growth rate of the two groups was high (0.91 ± 0.05), while that between fillet fat was intermediate (0.45 ± 0.17). Within the two groups, the genetic correlation of growth rate with fillet fat changed from positive (0.59 ± 0.14) in the SA group to negative (-0.45 ± 0.17) in the SW group, while the genetic correlation of growth rate with filet pigment changed from negative (0.33 ± 0.22) in the SA group to positive (0.62 ± 0.16) for the SW group. The parameters obtained at SW were obtained from a longitudinal Bayesian multivariate model for a truncated Gaussian trait (Ødegård et al., 2010; Kristjánsson et al., 2020) implemented through a Gibbs sampler procedure in DMU (Jensen et al., 2014). Prior to this study, no parameter estimate is available for traits recorded at about the same body weight for any fish or terrestrial animal species to authors knowledge. In a recent study (Kristjansson et al., 2021), the mentioned statistical model was used to analyse stochastic simulation SW data. It was found that for a population of 2000 animals six or more slaughter events are necessary to obtain an unbiased genetic correlation between growth rate and fillet fat.

This shows that genetic parameters of quality traits in Atlantic salmon are sensitive to whether they are estimated at the same age or the same body weight, and that substantial re-ranking of family breeding values for the quality trait is therefor expected when recorded at the same age or similar body weight. This knowledge is of great importance for a breeding program as the recording of the quality traits at the same body weight rather than at the same age is more in line with how the traits should be defined in the breeding objective (Kristjansson et al., 2020). However, performing repeated harvest of the test fish about the same body weight is laborious and stressful for the fish.

The objective of this study was, therefore, to investigate the possibility to obtain genetic parameters and breeding values for traits recorded on fish slaughtered at the same age that is comparable to those obtained when slaughtering the fish at the same body weight, thus making the recording of the data routinely less expensive and less invasive to the fish. This was done through the analyses of stochastic simulated SA data and of real SA data.

Material and methods

Three generations of data were generated by stochastic simulations using parameters obtained from the SA group (fish slaughtered and recorded at the same age) in a previous study (Kristjansson et al., 2020). In generation 0 (base population), 150 animals were generated (50 sires and 100 dams) using a nested mating design (each male to two females). Generation 1 was formed by mating the 50 sires and 100 dams from generation 0. Generation 2 was formed by mating randomly 50 sires and 100 dams from generation 1, but no mating of full sibs or half-sibs and thus no inbreeding. For the second generation, growth and fillet fat phenotypes were simulated for 420 days. The phenotypes used for the parameter estimation in this study were those from the time point when the average weight of the fish group was 4.4 kg, for comparison where the suggested models run on a real dataset of 2373 animals from two-year classes used in previous publication Kristjansson et al. (2020).

Growth curves

The mean body weight at each day $(\boldsymbol{j = 0, \ldots, 420})$ followed the Thermal Growth Coefficient (TGC) curve (Jobling, 2003):

$$\boldsymbol{BW_j = \left\{\left(\sqrt[3]{BW_0} + [(TGC/1000) \times (j \times t)]\right)\right\}^3} \qquad (1)$$

where the temperature $\boldsymbol{t = 10\ °C}$ and $\boldsymbol{TGC = 2.5}$ over the entire growth period and the mean starting weight $(\boldsymbol{BW_0})$ was 2 kg. The mean filet fat $(\boldsymbol{FF_0})$ at $\boldsymbol{BW_0}$ was assumed to be 10 % and was assumed to increase by 0.018 % unit per day as described by the following equation:

$$\boldsymbol{FF_j = \beta_0 + \beta_1 j} \qquad (2)$$

where $\beta_0 = 10$ % fillet fat and $\beta_1 = 0.018$ % unit increase per day j.

The additive genetic effect

For fish in generation 0, the animal additive genetic (co)variance effects $(\boldsymbol{u})$ for the animal traits fillet fat $(\boldsymbol{FF})$ and body weight $(\boldsymbol{BW})$ were drawn from a multivariate normal distribution using the Mass package (Venables and Ripley, 2002) in R (R Development Core Team, 2018). The assumed genetic covariance/correlation $(\boldsymbol{a})$ between the traits was 0.58; thus, the additive effect in the base population (generation 0, $\boldsymbol{t = 0}$) was as follows

$$\boldsymbol{u_{t=0\,(FF,BW)} = N_{t=0}(0, a) \quad \text{with} \quad a_{(FF,BW)} \sim \begin{bmatrix} 1 & 0.58 \\ 0.58 & 1 \end{bmatrix}} \qquad (3)$$

The additive genetic effect in generation 1 and 2 $(\boldsymbol{t = 1, 2})$ becomes

$$\boldsymbol{u_{t\,(FF,BW)} = 0.5\, u_{t-1\,(FF,BW)\ sire} + 0.5\, u_{t-1\,(FF,BW)\,dam} + N_{t=2(FF,BW)}(0, 0.5a)} \qquad (4)$$

where the $\boldsymbol{u_{t-1(FF,BW)}}$ is the genetic effects of the parents, and the latter part of equation 2 is the Mendelian sampling term.

Residuals

Each simulated animal had one record of $\boldsymbol{FF}$ and $\boldsymbol{BW}$ per day for 421 (0, 1, …,420) consecutive days (60 weeks). The residual variation of the traits $\boldsymbol{BW}$ (body weight, kg) and $\boldsymbol{FF}$ (fillet fat, %) was assumed to be unity, and the covariance/correlation 0.69. Between the days, the covariance/correlation was zero. Thus, the residual (co)variance matrix for day $\boldsymbol{j = 0, 1, \ldots, 420}$ becomes

$$\boldsymbol{e = \begin{bmatrix} s_0 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & s_{420} \end{bmatrix}} \qquad (5)$$

where $\boldsymbol{e}$ is 842 × 842 matrix since there are two traits within each day and the residual covariance/correlation matrix $\boldsymbol{s_j}$ between $\boldsymbol{BW}$ and $\boldsymbol{FF}$ within each day $\boldsymbol{j}$ is:

$$\boldsymbol{S_j \sim N\left(0, \begin{bmatrix} 1 & 0.69 \\ 0.69 & 1 \end{bmatrix}\right)} \qquad (6)$$

Phenotypes

The phenotypic variance becomes unity as both the variance of the additive and residual components are unity. The variances are then scaled using the growth curves and coefficient of variation for each day in the dataset to maintain the same heritability in all days in the dataset. The phenotypic $\boldsymbol{CV}$ for

$\boldsymbol{BW}$ was assumed to be 0.27 ($\boldsymbol{CV_{pBW}}$) and that for $\boldsymbol{FF}$ 0.1 ($\boldsymbol{CV_{pFF}}$). Heritability of $\boldsymbol{BW}$ was assumed to be 0.4 ($\boldsymbol{h^2_{BW}}$) and for FF to be 0.25 ($\boldsymbol{h^2_{FF}}$). The genetic coefficient of variation is defined as:

$$\boldsymbol{CV_a = \sqrt{h^2} \times CV_p} \qquad (7)$$

The same principle obtained the residual coefficient of variation.

For body weight, the phenotype for animal $\boldsymbol{i}$ at day **j** is the sum of the true additive genetic and the residual values plus the phenotypic mean of the population at day **j** as follows:

$$\boldsymbol{BW_{ij} = \overline{BW_j} + CV_{aBW}\overline{BW_j}\, u_{t=2(BW)i} + BW_{ij*}} \quad (8)$$

where the residual body weight $\boldsymbol{BW_{ij*}}$ is defined as:

$$\boldsymbol{BW_{ij*} = CV_{eBW}\overline{BW_j}N(0,e)_{BWij}} \quad (9)$$

The $\boldsymbol{BW}$ phenotypes used for the breeding values estimation (see next chapter) was at the day the mean $\boldsymbol{BW}$ of the population reached $\overline{\boldsymbol{BW}}_{\boldsymbol{j}} = 4.4\ kg$. For $\boldsymbol{FF}$ the phenotype for animal i at this timepoint $\boldsymbol{j}$ is:

$$\boldsymbol{FF_{ij} = \overline{FF}_j + CV_{aFF}\,\overline{FF}_j\, u_{t=2(FF)ij} + CV_{eFF}\,\overline{FF}_j\, N(0,e)_{FFij}} \qquad (10)$$

True breeding value

For $\boldsymbol{FF}$ the true breeding value of an animal $\boldsymbol{i}$ at day $\boldsymbol{j}$ is when each animal reaches 4.4 kg as follows:

$$\boldsymbol{TBV_{ijFF} = \overline{FF_j} + CV_{aFF}\,\overline{FF_j}\, u_{t=2(FF)i}} \quad (11)$$

The $\boldsymbol{TBV}$ for $\boldsymbol{BW}$ is the additive genetic part of equation 9 defined as:

$$\boldsymbol{TBV_{ijBW} = \overline{BW_j} + CV_{aBW}\overline{BW_j}\, u_{BWi2}} \quad (12)$$

For animal $\boldsymbol{i}$ at day $\boldsymbol{j}$ when the mean weight of the population reaches 4.4 kg.

Estimation of breeding values

The estimated breeding values for filet fat and body weight for all the 2000 simulated animals in generation 2 were obtained from a bivariate animal model(appropriate model described below in parentheses); for the observed $\boldsymbol{FF}$ and $\boldsymbol{BW}$ records (15); secondly where the observed $\boldsymbol{FF}$ records were pre-adjusted for the phenotypes of the $\boldsymbol{BW}$ (16) as well as for the residuals of $\boldsymbol{BW_*}$ (defined in equation 9) (17); thirdly where the phenotype of $\boldsymbol{BW}$(18) or residual of $\boldsymbol{BW_*}$ (19) was included as a covariate in the animal model for $\boldsymbol{FF}$.

Pre-adjusting fillet fat

The alternatives 16 and 17 above was performed by first fitting a linear model with $\boldsymbol{FF}$ as the response variable and phenotype of $\boldsymbol{BW}$ (or residual of $\boldsymbol{BW}$ defined in equation 9) as the explanatory variable:

$$\boldsymbol{FF_{ij} = \beta_0 + \beta_1 BW_{ij} + e} \quad (13)$$

where $\boldsymbol{\beta_1}(\boldsymbol{\beta_{1*}})$ is the regression coefficient of $\boldsymbol{FF_{ij}}$ on $\boldsymbol{BW_{ij}}(\boldsymbol{BW_{ij*}})$.

The pre-adjusted $\boldsymbol{FF_{ij}}$, in the further termed as $\boldsymbol{adjFF_{ij}}(\boldsymbol{adjFF_{ij*}})$, for animal i at the day j was calculated as:

$$adjFF_{ij} = FF_{ij} - \beta_1(BW_{ij} - \overline{BW_j}) \quad (14)$$

When pre-adjusting FF_{ij} by rBW to obtain $adjFF_{ij*}$ the BW_{ij} in equation 14 was replaced by BW_{ij*}

The statistical model for the simulated data

The estimated breeding values for the generation 2 animals for the traits FF, $adjFF$, $adjFF_*$ and BW was obtained from each of the following models when using the restricted maximum likelihood (REML) procedure in the DMU software (Jensen et al., 2014):

$$\begin{bmatrix} FF \\ BW \end{bmatrix} = \begin{bmatrix} \mu + Zu + e \\ \mu + Zu + e \end{bmatrix} \quad (15)$$

$$\begin{bmatrix} adjFF \\ BW \end{bmatrix} = \begin{bmatrix} \mu + Zu + e \\ \mu + Zu + e \end{bmatrix} \quad (16)$$

$$\begin{bmatrix} adjFF_* \\ BW \end{bmatrix} = \begin{bmatrix} \mu + Zu + e \\ \mu + Zu + e \end{bmatrix} \quad (17)$$

$$\begin{bmatrix} FF \\ BW \end{bmatrix} = \begin{bmatrix} \mu + \beta BW + Zu + e \\ \mu + Zu + e \end{bmatrix} \quad (18)$$

$$\begin{bmatrix} FF \\ BW \end{bmatrix} = \begin{bmatrix} \mu + \beta_* BW_* + Zu + e \\ \mu + Zu + e \end{bmatrix} \quad (19)$$

where

- μ Overall mean for the simulated phenotypes FF, $adjFF$, $adjFF_*$ and BW. For the real dataset (described in the chapter "Real dataset statistical models" is μ replaced by Xb where **b** is the interaction of sex and year class and **X** is the appropriate incidence matrix.
- u Vector of animal additive genetic effects, $u \sim N(0, A \otimes G_0)$ where **A** is the additive genetic relationship matrix among the animals in all three generations (0, 1 and 2) and G_0 is the additive genetic (co)variance matrix.
- β The regression coefficient of BW on FF.
- β_* Regression coefficient of BW_* on FF.
- e Vector of random residuals, where $e \sim N(0, I \otimes R_0)$. R_0 is the residual (co)variance matrix.
- Z The incidence matrix which links the additive genetic effect to their phenotypes.

The other variables in the above equations are defined above.

Real dataset statistical models

For each of the five studied models, the results from the stochastic simulation were compared with those obtained from the *SA* (slaughtered at the same age) group in (Kristjánsson et al., 2020); i.e. growth rate and fillet fat records from a total of 2373 fish of two-year classes (the offspring of 117

sires and 204 dams) slaughtered at an average body weight and fillet fat of 4.4 kg and 13.3 % (year class 1) and 4.6 kg and 17.3 % (year class). For these data, the residual growth rates ($\boldsymbol{rGR}$) were the residuals from the following univariate animal model:

$$\boldsymbol{GR_i = Xb + Zu + rGR_i} \qquad (20)$$

Where the fixed and random effects are described in the previous chapter. The regression coefficient for performing the pre-adjustment of fillet fat for growth rate and residual of growth rate was obtained from the two following models:

$$\boldsymbol{FF = Xb + Zu + \beta_1 GR + e} \qquad (21)$$

$$\boldsymbol{FF = Xb + Zu + \beta_{1*} rGR + e} \qquad (22)$$

The pre-adjustment was performed as:

$$\boldsymbol{adjFF_{ij} = FF_{ij} - \beta_1\left(GR_{ij} - \overline{GR_j}\right)} \qquad (23)$$

$$\boldsymbol{adjFF_{ij*} = FF_{ij} - \beta_{1*}\left(rGR_{ij} - \overline{rGR_j}\right)} \qquad (24)$$

The above-defined phenotypes were analysed with the same models as used for the simulated data, but in which the trait $\boldsymbol{BW}$ was replaced by $\boldsymbol{GR}$.

The overall estimated breeding values

Separately for the simulated and the real data, an overall estimated breeding value ($\hat{\boldsymbol{s}}_{\boldsymbol{ij}}$) for the two traits for each animal for each of the five animal models (15-19) was calculated as:

$$\hat{\boldsymbol{s}}_{\boldsymbol{ij}} = \boldsymbol{a_1}\,\hat{\boldsymbol{u}}_{\boldsymbol{1i}} + \boldsymbol{a_2}\hat{\boldsymbol{u}}_{\boldsymbol{2i}} \qquad (25)$$

where $\hat{\boldsymbol{u}}_{\boldsymbol{1i}}$ and $\hat{\boldsymbol{u}}_{\boldsymbol{2i}}$ is the estimated breeding value for animal $\boldsymbol{i}$ for growth rate ($\boldsymbol{BW}$ for the simulated data and $\boldsymbol{GR}$ for the real data) and fillet fat, respectively; and $\boldsymbol{a_1}$and $\boldsymbol{a_2}$ are the relative economic weights given to each of the traits. The economic weight for growth rate was set equal to $\boldsymbol{a_1}$**=1,** while for fillet fat, the following different economic weights were used: -4, -3, -2, -1, 0, +1, +2, +3, +4; where the negative, zero and positive weights imply alternative breeding objective, i.e., to reduce, keep constant or increase the filet fat in the population, respectively.

As reliable fillet fat records may be difficult to obtain on the live breeding candidates, an alternative overall estimated breeding value was calculated:

$$\hat{\boldsymbol{s}}_{\boldsymbol{ij}} = \boldsymbol{a_1}\,\hat{\boldsymbol{u}}_{\boldsymbol{1i}} + \boldsymbol{a_2}\hat{\overline{\boldsymbol{u}}}_{\boldsymbol{2i}} \qquad (26)$$

where $\hat{\overline{\boldsymbol{u}}}_{\boldsymbol{2i}}$is the estimated family breeding values for fillet fat.

The overall true breeding value

For the simulated data, an overall true breeding value was calculated using the same two equations as for the overall estimated breeding values (25), but in which the estimated breeding values were replaced with their true value as defined in equation 11 and 12.

Evaluation criteria for the simulated data

The bias and accuracy of the estimated breeding values were used as the two evaluation criteria of the studied models for the simulated data only.

The bias was defined as:

$$\boldsymbol{Bias} = \frac{\sum(\boldsymbol{TBV} - \hat{\boldsymbol{u}})}{\boldsymbol{n}} \qquad (\mathbf{27})$$

where $\boldsymbol{TBV}$ is the true breeding value defined in equation 11 and 12, and $\boldsymbol{EBV}$ is the estimated breeding value defined in equations 15-19 for both traits. For $\boldsymbol{FF}$ was the estimated fixed effect was added to the $\boldsymbol{EBV}$ since the $\boldsymbol{TBV}$ for $\boldsymbol{FF}$ included $\boldsymbol{FF}$ curve value at 4.4 kg. Value of $\boldsymbol{n = 2000,}$ which is the number of animals.

The accuracy of the estimated breeding values, i.e., the correlation between $\boldsymbol{TBV}$ and $\boldsymbol{EBV}$ was calculated as:

$$\boldsymbol{Accuracy} = \frac{\boldsymbol{cov}(\boldsymbol{TBV}, \hat{\boldsymbol{u}})}{\boldsymbol{sd}(\boldsymbol{TBV})\boldsymbol{sd}(\hat{\boldsymbol{u}})} \qquad (\mathbf{28})$$

Where the standard error of the true and estimated breeding values is $\boldsymbol{sd}(\boldsymbol{TBV})$ and $\boldsymbol{sd}(\hat{\boldsymbol{u}})$ respectively.

Prediction of genetic gain

An evaluation of how to best perform the adjustment of the simulated $\boldsymbol{FF}$ records for their corresponding $\boldsymbol{BW}$ records was based on the predicted genetic gain of each of the two studied traits when selecting some of the highest-ranking animals as parents for the generation 3 based on an overall breeding (index) value obtained by assigning a different set of relative weights to the two estimated breeding values ($\boldsymbol{EBVs}$) of the two traits.

A prediction of the genetic gain from generation 2 to 3 was obtained by first selecting the five individuals within each of the generation 2 families with the highest overall breeding value (total of 500 individuals from the 100 families), after which the 150 individuals with the highest overall breeding value among these 500 individuals were selected as the parents for generation 3. The predicted genetic gain from generation 2 to 3 for each trait as well as for the overall breeding values was calculated as the difference in the mean estimated breeding value of the 150 selected individuals as a deviation from the overall all mean breeding value of all generation 2 animals; and which was performed for each of the five tested statistical models.

For the simulated data, the reported results are the mean values of 30 simulated replicates for each of the investigated scenario.

For the real data were selected the best 6 individuals based on the overall breeding value within the 204 families resulting in 1206 individuals (some families had less than 6 per family with a complete record for both $\boldsymbol{FF}$ and $\boldsymbol{GR}$) were made available for selection where 200 best were selected based on the overall breeding value to have similar proportion selected in the real data as in the simulated data.

Results

Common environmental effect

In Kristjansson et al. (2020), the random effect common for full sibs was significant for all the SA-group traits. Due to convergence problems of parameter estimates of the real data for some of the models, the effect common environmental was dropped from all five studied models. For the real data, the only model that converged with the common environmental effect included was the bivariate model for ***FF*** pre-adjusted for ***GR***, for which the variances components were found to be 0.62/0.07/1.32 (additive genetic/effect common to full sibs/residual) while the estimates without the effect common for full sibs were 0.74/1.24 (additive genetic/residual) as also seen in Table 2.

Effect of adjustment methods on regression coefficients and variances

Table 1 shows that the magnitude of the estimated regression coefficients obtained from the real data for performing the pre-adjustment of ***FF*** for ***GR*** or ***rGR*** are different for the interaction of the fixed effects year-classes and sex, therefore have to be obtained for each set of data.

Correlations between the EBVs of the different adjustment methods

Pre- and covariate adjustment of fillet fat (***FF***) for body weight (simulated data) and growth rate (real data) resulted in a similar reduction of the genetic variance of ***FF***. In contrast, pre-and covariate adjustment of fillet fat (***FF***) for residual of body weight (simulated data) or residual growth rate (real data) resulted in a marginal reduction in the genetic variance (Table 2).

The medium correlations between the ***EBVs*** of the non-adjusted ***FF*** with the pre-and covariate-adjusted ***FF*** for ***BW*** show that non-adjusted and adjusted ***FF*** values are quite different traits.

The unity correlation between the ***EBVs*** (and between their residuals) of the pre-and covariate-adjusted ***FF*** values for both the simulated and real data shows that these two adjustment methods give identical results (Table 2). The very high correlations between the ***EBVs*** of no-adjusted with the pre-adjusted and the covariate-adjusted ***FF*** for ***rBW*** or ***rGR*** strongly indicates that adjustment of ***FF*** for ***rGR*** or ***rBW*** is of no practical importance (Table 2).

Accuracy, genetic and residual correlation

Figure 1 shows that when ***FF*** of simulated data were pre-adjusted or covariate-adjusted for ***BW***, the genetic correlation between ***BW*** and adjusted ***FF*** changed from 0.57 (no-adjustment) to -0.28, the residual correlation changed from 0.68 (no-adjustment) to 0.15, and the accuracy of ***EBV*** of ***FF*** increased from 0.39 (no adjustment) to about 0.63. When using ***rBW*** as a covariate, the residual correlation changed from 0.69 (no adjustment) to 0.50, while the genetic correlation and the accuracy of the ***EBVs*** of ***FF*** changed very little. The latter was also the case when ***FF*** was adjusted by ***rBW***, while for that case, the residual correlation was zero.

Figure 2 shows that when ***FF*** of simulated data were pre- or covariate-adjusted for ***GR*** the genetic correlation between ***GR*** and adjusted ***FF*** changed from 0.70 to -0.05. In contrast, when ***FF*** was pre- or covariate adjustment for ***rGR*** the genetic correlation changed marginally from 0.70 to 0.78, while the residual correlation changed from 0.66 (no-adjustment) to -0.50 (pre-adjusted) and -0.23 (covariate-adjusted).

Expected genetic gain – simulated data.

Figure 3 (upper) shows that when performing family selection for reduced ***FF*** (and simultaneously combined selection increased ***BW***), no adjustment or pre-or covariate adjustment of ***FF*** for ***BW*** produced a similar genetic gain in ***FF*** and higher genetic gain than when performing pre- or covariate adjustment for ***rBW***. However, when performing family selection for increased ***FF*** (and increased growth rate), pre-or covariate adjustment of ***FF*** for ***BW*** or pre-adjustment for ***rBW*** produced a similar genetic gain in ***FF*** and higher genetic gain than when performing covariate adjustment of ***FF*** for ***rBW*** and no adjustment which produced the lowest genetic gain in ***FF***.

Figure 3 (lower) shows that when ***FF*** records were assumed to be also recorded on the breeding candidates, adjustment of ***FF*** had a marginal effect on the genetic gain in ***FF*** when selecting for reduced ***FF***. However, when selecting for increased fillet fat, pre-or covariate adjustment of ***FF*** for ***BW*** produced the highest genetic gain in ***FF***, particularly when the economic weight given to *FF* increased relative to that given to ***BW***.

When selection is for increased ***BW*** only (zero economic weight on ***FF***) the true correlated response in ***FF*** is about -0.2 %-units (Figure 3) which can be explained by the estimated negative genetic correlation between ***BW*** and ***FF*** seen after pre- or covariate adjustment of ***FF*** for ***BW*** (Figure 1).

Figure 4 (upper) shows that when performing family selection for reduced fillet fat (and simultaneously combined selection for increase ***BW***), pre-adjustment or covariate adjustment of ***FF*** for ***BW*** yielded a relative marginal reduction in genetic gain for growth rate, particularly when compared to performing pre- or covariate adjustment of ***FF*** for ***rBW*** or no adjustment for which the genetic gain decreased as the economic weight given to ***FF*** increased relative to that given to ***BW***. Contrary, when performing family selecting for increased ***FF***, pre-and covariate adjustment of ***FF*** for ***rBW*** or no adjustment produced the highest genetic gain in ***BW***, while pre- or covariate adjustment of ***FF*** for ***BW*** yielded a reduced gain in ***BW*** with increasing economic weight on ***FF***. Figure 4 (lower) shows that the effects seen in the upper figure were more pronounced when ***FF*** were assumed to be also recorded on the breeding candidates as compared to only on the sibs of the candidates.

Figure 5 shows that when selecting for reduced ***FF*** (and simultaneously combined selection for increased ***BW***) pre-and covariate adjustment of ***FF*** produced the highest overall genetic gain, while when performing selection for increased ***FF*** pre- and covariate adjustment of ***FF*** for ***rBW*** or no adjustment produced the highest overall genetic gain. Figure 5 (lower) shows that the effects seen in the upper figure were more pronounced when ***FF*** were assumed to be also recorded on the breeding candidates as compared to on only the sibs of the candidates. As expected, the overall genetic gain increased with increasing economic weight put on ***FF***.

Worth to notice is that when selecting for reduced ***FF*** (or increased ***FF***) the suboptimal adjustment methods produced higher overall genetic gain when an economic weight of zero was given to ***FF*** as compared to -1 (+1).

Expected genetic gain – real data.

Figure 6 shows that when selecting for increased filet fat (and simultaneously for increased growth rate), pre-and covariate adjustment of ***FF*** for ***GR*** produced a lower genetic gain in ***FF*** as compared to the three other adjustment methods (including no adjustment) that all produced similar genetic gain, and thus not in accordance with what was found for the simulated data.

When selection is for increased ***BW*** only (zero economic weight on ***FF***), the correlated estimated genetic gain in ***FF*** is about +1 %-units (Figure 6) which can be explained by the positive genetic correlation between ***BW*** and ***FF*** of the observed non-adjusted ***FF*** values. However, based on the ***EBVs*** of the ***FF*** pre- or covariate-adjusted for ***BW***, the correlated genetic gain in ***FF*** is zero. In the real data, the true correlated response is not possible to estimate as the ***TBVs*** for ***FF*** are not known.

Figure 7 shows that when selecting for increased ***FF*** (and simultaneously for increased growth rate), pre-and covariate adjustment of ***FF*** for ***GR*** produced a lower genetic gain in growth rate as compared to the three other adjustment methods (including no adjustment) that all produced similar genetic gain, and thus in accordance with what was found for the simulated data.

Figure 8 shows that the ranking of the overall genetic gains for the different adjustment methods over the range of economic weights assigned to ***FF*** was similar to those found for the simulated data.

Discussion

The objective was to find the best method to simultaneously select for increased growth rate (***GR***) and fillet fat (***FF***) when the tested animals are recorded at a desired average body weight at the same age. This was investigated through a stochastic simulation study and real data and by performing five different adjustment methods (including no adjustment) of ***FF*** for the body weight (***BW***) of the fish. Each of the methods was evaluated by the estimated (co)variances of the two studied traits and their expected and overall true (simulated data) and estimated (real data) genetic gain when assigning a fixed positive economic weight to the growth rate and varying negative zero and varying positive economic weights to ***FF*** thus reflecting a breeding goal objective to decrease, keep constant, or increase ***FF***. The estimated expected genetic gain was that for one generation of selection and where ***GR*** was assumed to be recorded on all the breeding candidates while ***FF*** was assumed to be recorded either on the sib of the candidates only or also on the breeding candidates.

Table 1 shows the estimated regression coefficients for performing the pre-adjustment of ***FF*** by ***rBW/BW*** (simulated data) or ***rGR / GR*** (real data) for the four studied models. The magnitude of the real data estimates obtained from the different year-class by sex combinations shows that estimates need to be obtained for each data set.

Adjusting ***FF*** for ***BW*** or ***GR*** caused, as expected, a reduction in genetic variance because of the genetic correlation of ***FF*** with ***BW*** (Figure 1) and ***GR*** (Figure 2). Reduced genetic variance is expected to cause reduced genetic gain. On the other hand, adjusted ***FF EBV*** had higher accuracy than non-adjusted ***EBV*** (Figure 1), which may compensate for the reduced genetic variance without a reduction in the genetic gain. The adjustment also changed the estimated genetic correlation between ***FF*** and ***BW*** / ***GR*** from positive to negative. Hence, selecting for non-adjusted ***FF EBV*** means to select for ***EBV*** with a positive correlation to growth, while selecting for ***BW*** -adjusted ***FF EBV*** means to select for ***EBV*** with negative correlation to growth. This correlation will affect the genetic gain in a multi-trait selection scenario. To select the best adjustment method to maximise genetic gain, there is a need to evaluate the gain for each of the traits in the selection index, to take into account not only the accuracy of the ***EBVs*** and the genetic variances but also the genetic correlation between the traits. In this study, this was illustrated when performing one generation simultaneously selection for the two studied traits ***FF*** and ***GR*** on an overall breeding value of the traits. Economic weight for ***GR*** was set to 1, while the economic weight for ***FF*** was varied between -4 to +4 to cover a range of possible values ***FF*** could have, as economic weights for ***FF*** in Atlantic salmon or any other farmed fish species have not been derived to authors knowledge.

It was found that the pre-and covariate adjustment of $\boldsymbol{FF}$ for $\boldsymbol{BW}$ or $\boldsymbol{GR}$ (real data) produced very similar results. Furthermore, no adjustment of $\boldsymbol{FF}$ or pre-or covariate adjustment of $\boldsymbol{FF}$ for $\boldsymbol{rBW}$ or $\boldsymbol{rGR}$ (real data) gave very similar result and thus of no practical importance to adjust $\boldsymbol{FF}$ for $\boldsymbol{rBW}$ or $\boldsymbol{rGR}$. Consequently, to pre-adjust $\boldsymbol{FF}$ only for the environmental/residual effect of body weight and thus maintain the genetic variation in $\boldsymbol{FF}$ did not work as expected. Therefore, in the following, we will only discuss the implication of adjusting $\boldsymbol{FF}$ for $\boldsymbol{BW}$ as compared to no adjustment of $\boldsymbol{FF}$ for $\boldsymbol{BW}$.

When simultaneously selection for increased growth rate and reduced $\boldsymbol{FF}$ was performed, adjustment of $\boldsymbol{FF}$ for $\boldsymbol{BW}$ gave higher genetic gain for $\boldsymbol{FF}$ and substantial higher genetic gain for $\boldsymbol{GR}$ as compared to practising no adjustment of $\boldsymbol{FF}$ for $\boldsymbol{BW}$. However, when performing selection for increased growth rate simultaneously and increased $\boldsymbol{FF}$, covariate adjustment of the $\boldsymbol{FF}$ for $\boldsymbol{BW}$ gave higher genetic gain for $\boldsymbol{FF}$ but a substantial lower genetic gain for $\boldsymbol{GR}$. In the latter case, it can therefore be recommended to not adjust $\boldsymbol{FF}$ for $\boldsymbol{BW}$ as this will give the highest overall genetic gain for the two traits.

In this study, the heritability for body weight in the simulated dataset was set to 0.4 and heritability for $\boldsymbol{FF}$ was set to 0.25. In a sensitivity study (results not shown), the heritability was set to 0.25 or 0.4 for both traits; the trend was the same as those reported in Figure 1, 3, 4 and 5.

The different adjustment models' sensitivity to the magnitude of the regression coefficient of $\boldsymbol{FF}$ on the age (or body weight) was also tested (results not shown). In a previous study, the magnitude of the slope of the fat curve had a significant effect on the genetic correlation between growth rate and $\boldsymbol{FF}$ recorded at about the same body weight of the fish, since there was a marginal change in genetic and residual correlations using a various slope of the fillet fat curve the slope defined in equation 2 was used for the selection differential evaluations. By increasing the FF curve slope, the selection differences increase for FF (figure not shown), but the trends are the same as shown in Figure 3,4 and 5. Therefore, this study found that for positive slopes, adjustment of $\boldsymbol{FF}$ for $\boldsymbol{BW}$ was the method to use when selecting for reduced body weight and no adjustment for $\boldsymbol{FF}$ when selecting for increased $\boldsymbol{FF}$.

When applying the pre-correction methods in the simulation dataset, the heritability increases, as seen in table 2, irrespective of pre-correcting/covariate methods. Thus, the residual variation was reduced more than the additive variation for both the simulated and real data. For the $\boldsymbol{rBW}$ pre-correcting/covariate in the simulation data, the residual is reduced more than in the real data, probably since the actual $\boldsymbol{rBW}$ is used in the simulated data, whereas the $\boldsymbol{rGR}$ is an estimate of the residual.

The parameter estimates from a previous publication (Kristjánsson et al., 2020) indicate that if the breeding goal is to increase growth rate/body weight and marginally decrease fillet fat, it may not be necessary to record or select for fillet fat due to the negative genetic correlation between growth rate and fillet fat registered at same weight individuals.

In this study, we performed simultaneous selection for two traits, $\boldsymbol{GR/BW}$ and one quality trait ($\boldsymbol{FF}$). We assumed that the magnitude of the recorded quality trait is dependent on age and weight and that the breeding goal is to improve quality at a given weight, while data is only available when the whole group of test fish is slaughtered at a chosen time point at the same age at which they vary in their actual body weight. This is probably a relevant scenario for a number of quality traits. We found that pre-adjustment for body weight had a minor effect on the genetic gain for $\boldsymbol{FF}$ itself, probably because increased accuracy and decreased genetic variance act in different directions and to a large extent compensate each other. However, the change in the genetic correlation between $\boldsymbol{GR}$ and $\boldsymbol{FF}$, from a

positive to a negative value when adjusting $\boldsymbol{FF}$ for $\boldsymbol{GR}$, affected the genetic gain for $\boldsymbol{GR}$. Since quality traits, in general, are expected to be affected by body weight, a change in genetic correlation after adjusting for body weight will probably be present also for other quality traits, as shown in Kristjansson et al. (2020). To perform a multi-trait selection for several correlated traits will require an estimation of total genetic gain. The method described here can be extended to include more and other quality traits, given that the genetic parameters of the measured traits and the breeding goal traits are known or assumed to be known.

Conclusion

When growth rate and fillet fat in Atlantic salmon are recorded at the same age, and the breeding goal is to reduce fillet fat and increase growth rate, using the body weights to adjust the fillet fat records give a higher genetic gain in growth rate and a minor reduction in fillet fat as compared to performing no adjustment of the fillet fat records. However, if the breeding goal is to increase both traits, no adjustment of the fillet fat records for body weight give higher genetic gain than adjusting the fillet fat records for body weight.

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Tables

Table 1 Estimated regression coefficients of fillet fat on body weight (Bw) or residual body weight (rBw) for simulated data, and of fillet fat on growth rate (Gr) or residual growth rate (rGr) for real data nested within fixed effects, obtained from a single trait model with the overall mean (simulated data) or year-class x sex (real data, M=Male, F=Female) as the fixed effect and with an animal additive genetic as a random effect

Simulated data		Real data			
Trait	**Estimate ± see**	**Trait**	**Year-class**	**Sex**	**Estimate ± see**
Bw	0.69 ± 0.03	***Gr***	1	M	1.21 ± 0.04
				F	1.38 ± 0.05
			2	M	0.76 ± 0.05
				F	1.10 ± 0.07
rBw	0.82 ± 0.02	***rGr***	1	M	1.81 ± 0.06
				F	2.09 ± 0.08
			2	M	1.14 ± 0.09
				F	1.75 ± 0.11

Table 2. Estimates of genetic and residual variances for fillet fat(FF) (on the diagonal); of correlations between the estimated breeding values for FF obtained from the five different models (below the diagonal); and of the correlations between the residuals of the different models (above the diagonal). The two lines are the estimates from the stochastic simulation study (upper) and the real (lower) data.

	Trait	No adjustment	Bw/Gr		rBw/rGr	
Adjustment method			**Pre-adjust.**	**Covariate**	**Pre-adjust.**	**Covariate**
No adjustment	Bw	0.40/1.22	-	-	-	-
	Gr	1.64/2.28	0.78	0.78	0.36	0.59
Pre-adjust.	Bw	0.55	0.28/0.66	-	-	-
	Gr	0.61	0.78/1.24	1.00	0.86	0.96
Covariate	Bw	0.50	1.00	0.30/0.65	-	-
	Gr	0.61	1.00	0.78/1.24	0.90	0.96
Pre-adjust.	rBw	0.94	0.57	0.52	0.41/0.64	-
	rGr	0.97	0.67	0.66	1.49/0.89	0.97
Covariate	rBw	0.99	0.58	0.58	0.98	0.40/0.83
	rGr	0.97	0.67	0.67	1.00	1.55/0.89

Figures

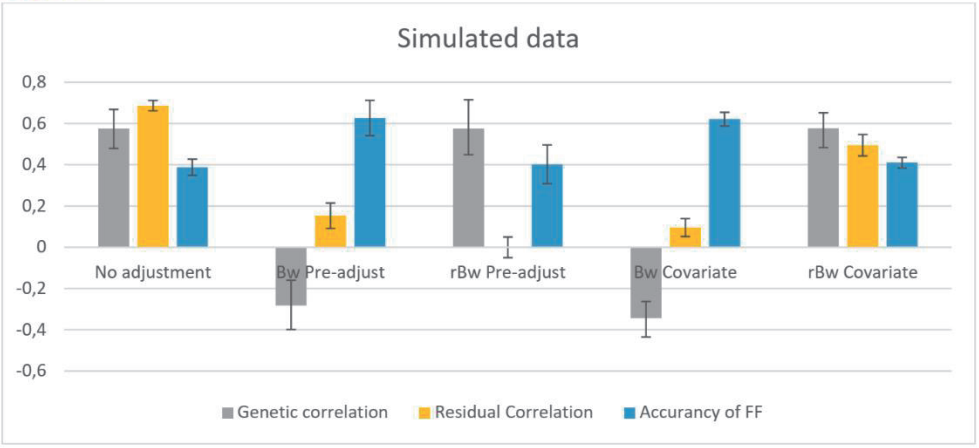


Figure 1 Estimates of genetic and residual correlation between body weight (Bw) and fillet fat (FF) from the five different models of the simulated data, and the accuracy of the estimated breeding values for FF; means of 30 replicates and where the bars are the standard deviations of the 30 replicates.

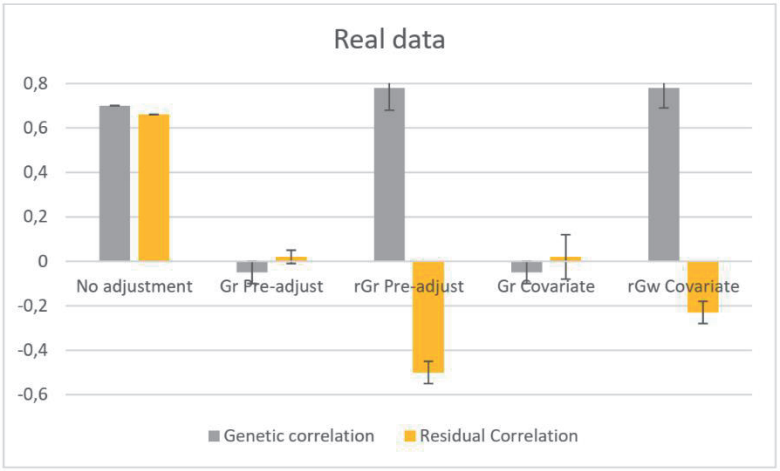
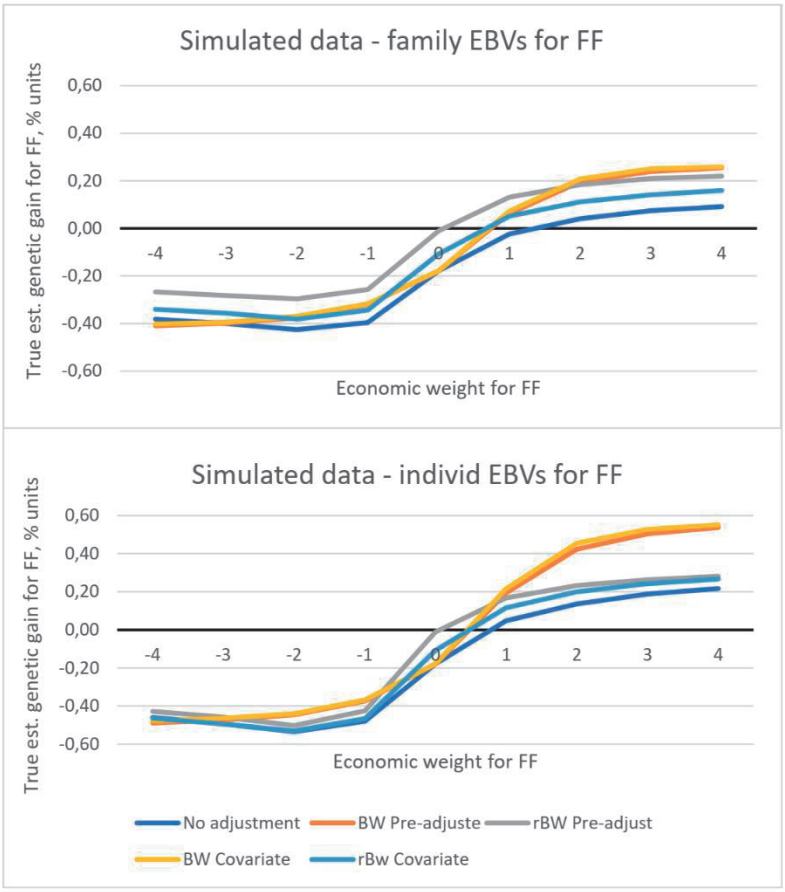


Figure 2. Estimates of genetic and residual correlation between growth rate (Gr) and fillet fat (FF) from the five different real data models, and where the bars indicate the standard error of the estimates.

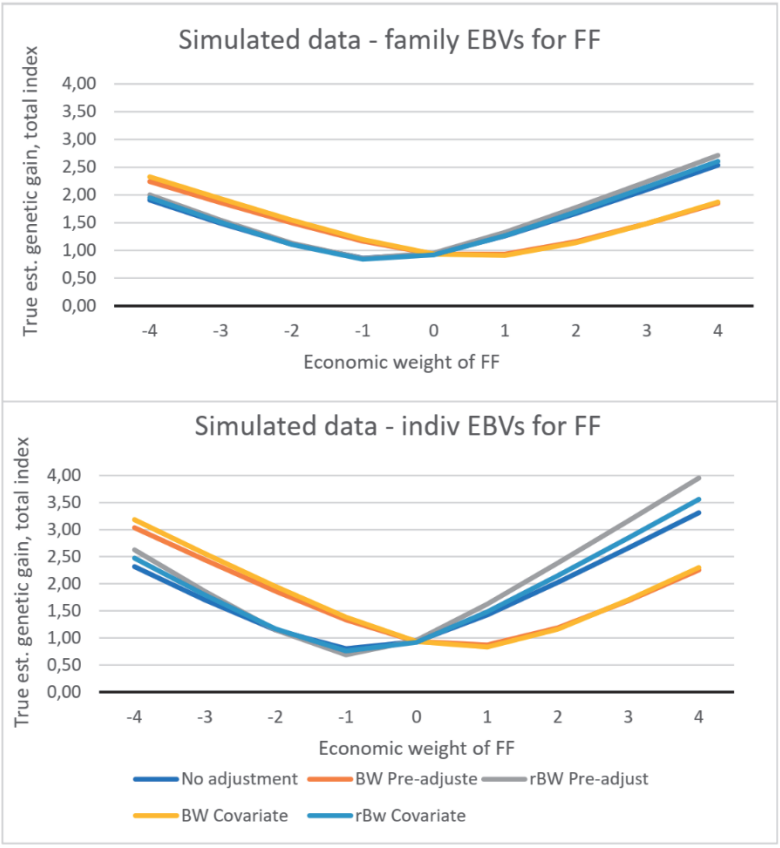


452

453 *Figure 3. Estimates of true genetic gain for filet fat(FF) (%-units) when performing selection on an overall breeding value*
454 *for growth rate and fillet fat for different relative economic weights on body weight (+1) and family (upper figure) or*
455 *individual (lower figure) breeding value for fillet fat (-4 to +4).*

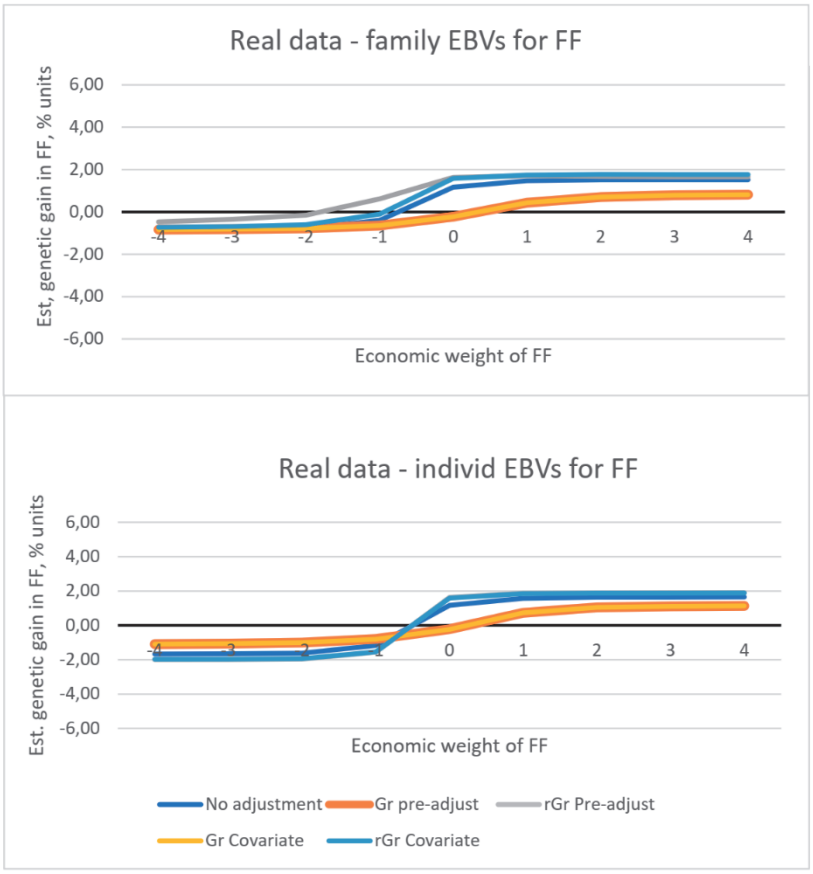
456

457 *Figure 4. Estimates of true genetic gain for body weight(BW)(kg) when performing selection on an overall breeding value for*
458 *growth rate and fillet fat for different relative economic weights on body weight (+1) and family (upper figure) or individual*
459 *(lower figure) or breeding value for fillet fat (-4 to +4).*



460

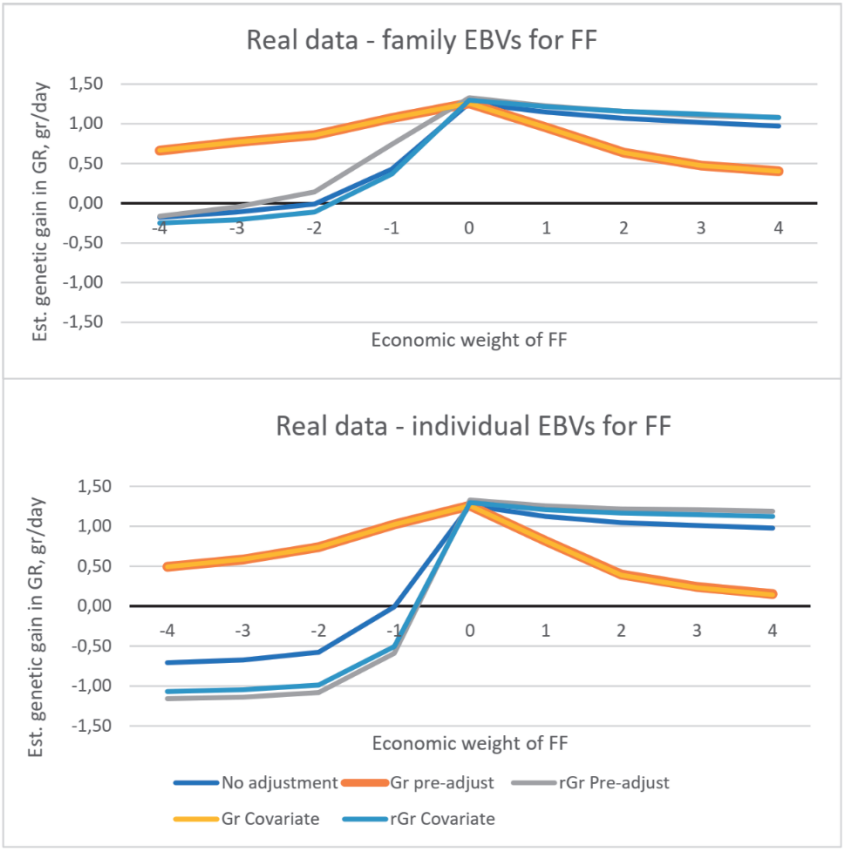
461 *Figure 5. Estimates of true overall genetic gain when performing selection on an overall breeding value for body weight and*
462 *fillet fat for different relative economic weights on body weight (+1) and family (upper figure) or individual (lower figure) or*
463 *breeding value for fillet fat (-4 to +4).*



464

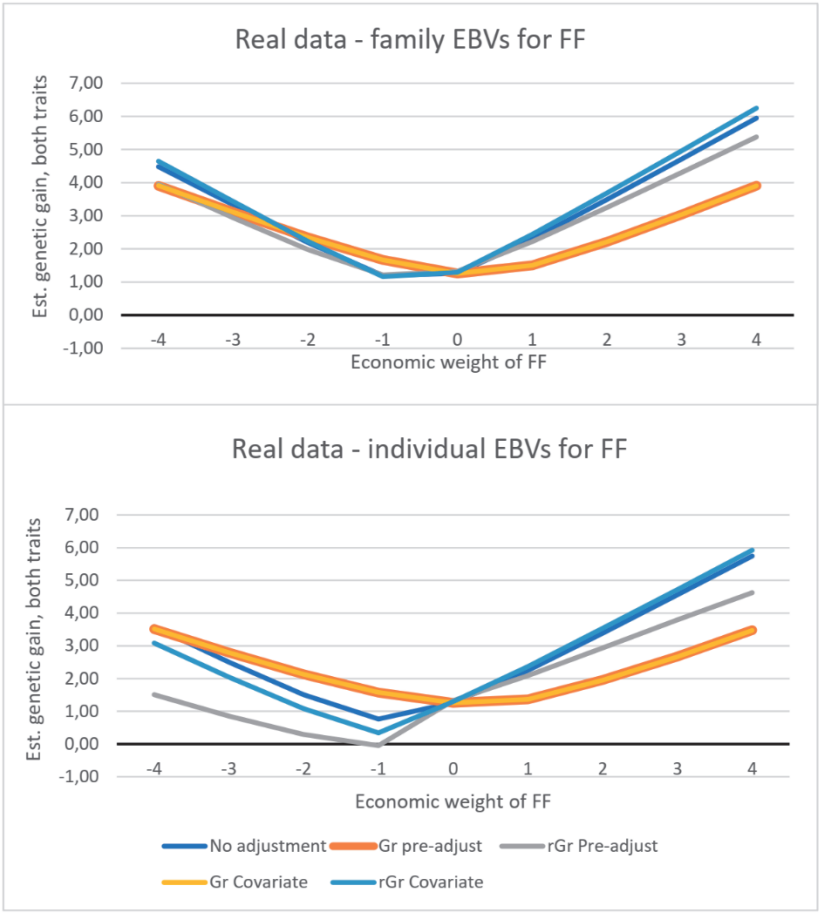
465 *Figure 6. Estimates of selection differential for filet fat (%-units) in real data when performing selection on an overall*
466 *breeding value for growth rate and fillet fat for different relative economic weights on growth rate (+1) and family (upper*
467 *figure) or individual (lower figure) breeding value for fillet fat (-4 to +4).*

468



469

470 *Figure 7 Estimates of selection differential for growth rate (g/day) in real data when performing selection on an overall*
471 *breeding value for growth rate and fillet fat for different relative economic weights on growth rate (+1) and family (upper*
472 *figure) or individual (lower figure) or breeding value for fillet fat (-4 to +4).*



473

474 *Figure 8 Estimates of overall genetic gain when performing selection on an overall breeding value for growth rate and fillet*
475 *fat for different relative economic weights on growth rate (+1) and family (upper figure) or individual (lower figure)*
476 *breeding value for fillet fat (-4 to +4).*

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