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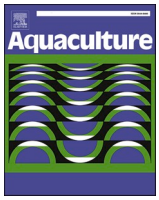

# Validation and genetic parameters of the X-ray method for phenotyping individual feed intake in Atlantic salmon

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ABSTRACT

Feed efficiency is a highly desirable breeding goal trait as it can potentially reduce the relative economic cost of feed and concurrently reduce the environmental footprint of fish production. However, recording feed intake is a bottleneck in Atlantic salmon production. We recorded feed intake in 700 Atlantic salmon parr from 34 full sibling families using the X-ray method, where fish were fed feed containing radio-opaque beads and subsequently X-ray imaged one time after a full meal corresponding to the daily ration. In parallel, we cultured siblings from the same 35 families in duplicate family tanks of 25 individuals per tank and recorded the daily feed intake of each family at the tank level, which is known as the gold standard tank-based method. The heritability estimate for daily feed intake in Atlantic salmon using the X-ray method was significantly different from zero (0.19 ± 0.06) and was genetically correlated to growth-related traits ($r_g$ = 0.48–0.81). Daily feed intake at the family level with the X-ray method was highly genetically correlated to the daily feed intake traits using the tank-based feeding method at 0.78–0.82, depending on whether the comparison was made at a common time, common weight, or cumulative feed intake for the entire period. Whilst the X-ray method holds promise for research on the genetic background of feed intake and feed efficiency, more studies are needed to investigate the feasibility during the sea phase of Atlantic salmon production.

## 1. Introduction

The Atlantic salmon industry faces the challenges of remaining a profitable enterprise while reducing the carbon footprint of production. Feed plays a key role in the economic performance and environmental sustainability of Atlantic salmon production, with the cost of feed accounting for over 50% of the total production cost of farmed Atlantic salmon (Iversen et al., 2020) and 85% of the carbon footprint (Ziegler et al., 2021). Improving the amount of edible product relative to the feed input of Atlantic salmon (i.e. feed efficiency) offers considerable potential to improve both profitability and environmental sustainability (Kause et al., 2006b).

Selective breeding is one possible strategy for improving the feed efficiency of Atlantic salmon production. There is evidence of genetic variation in feed efficiency of Atlantic salmon (Dvergedal et al., 2019; Kolstad et al., 2004; Thodesen et al., 2001; Thodesen et al., 1999) as well as other salmonids (Hatlen et al., 1997; Henryon et al., 2002; Kause et al., 2006a; Kinghorn, 1983; Walker et al., 2012), and that feed efficiency is favourably genetically correlated to the growth rate. Consequently, selection for increased growth rate is expected to result in a favorable correlated response in feed efficiency but will not access all the genetic variation in feed efficiency. However, direct selection for improved feed efficiency requires individual feed intake and concurrent growth records on thousands of full- and half-sibs with known genetic relationships under conditions similar to where their offspring are expected to perform (Falconer and Mackay, 1996). Widespread use of genomic selection in Atlantic salmon breeding programs has offered up the possibility to select for novel traits, in particular traits that are traditionally expensive or difficult to measure in large cohorts like feed efficiency.

It is extremely challenging to record individual phenotypes for feed intake and thus determine feed efficiency, particularly throughout the life stages of Atlantic salmon and under commercial conditions (Knap and Kause, 2018). The ‘gold standard’ for recording feed intake in aquaculture species, is experiment unit (tank, pen, or aquaria) based feeding, where the amount of feed consumed is the difference between

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the amount of feed given and the recovered uneaten (wasted) feed from the unit (Helland et al., 1996). This method is highly accurate and precise if conducted with accurate automated feed delivery, routine recovery tests, a combination of high-quality extruded pellets and a waste collection system that can separate uneaten feed and feces (Helland et al., 1996; Madrid et al., 1997). In principle, this method can generate individual-level phenotypes, by housing a single individual per tank or aquaria as has been demonstrated in numerous other aquatic species (Besson et al., 2022; Besson et al., 2019; Dai et al., 2019; Dvergedal et al., 2022; Rodde et al., 2021; Silverstein, 2006). However, commercial aquaculture production is based on large groups of individuals in tanks or cages and mounting evidence suggests the growth (Silverstein, 2006), feed intake (Dai et al., 2019), and feed efficiency (Rodde et al., 2021) differ under individual or group feeding systems. In many aquaculture finfish species including Atlantic salmon, many if not all individuals will not consume feed or have greatly reduced feed intake if housed alone (B. Gjerde personal communication, 2018; Dvergedal et al., 2022), making individual feed intake records using the tank-based feeding method practically unfeasible in Atlantic salmon.

In Atlantic salmon, groups of full sibling families have been reared in replicate tanks, and feed intake recorded at the family level using the tank-based feeding method (Kolstad et al., 2006; Thodesen et al., 1999). This has demonstrated between 31 and 77% of the total variation in feed efficiency is due to differences between families (Kolstad et al., 2006; Thodesen et al., 1999). The efficiency of recording family-level feed intake for selection purposes has been called into question as large amounts of tank resources and the size of tanks place limitations on the number of families and size the fish grow to (Kolstad et al., 2005), making this a costly and laborious method which only access half the additive genetic variation (between families).

An alternative method for individual recording of feed intake in large numbers of group-housed fish, is the X-ray method (Kause et al., 2006a; Walker et al., 2012). This method estimates individual-level feed intake by including radio-opaque markers such as beads or iron particles within the pelleted feed. The mass of ingested feed during a meal is inferred from a count of the number of bead particles within the digestive tract from an X-ray image of each fish and a mass-to-bead number calibration standard (Jobling et al., 1993; Talbot and Higgins, 1983). The daily feed intake recorded by the X-ray method is heritable in rainbow trout (Kause et al., 2006a) and Chinook salmon (Scholtens et al., 2023; Walker et al., 2012), however, estimates for Atlantic salmon are still lacking. Drawbacks of this method are that manually counting the beads from the X-ray images is laborious, tedious, and time-consuming and the biggest bottleneck to obtaining feed intake records on large cohorts of fish. Since the method records a single snapshot measurement in time, repeated measurements encompassing the entire period of growth in question are required. However, a reliable estimate of the number of X-ray records needed to approximate cumulative feed intake over a sufficiently long growth period has not been determined due to the lack of methods for obtaining cumulative feed intake for communally reared individuals.

The objectives of the current study are to 1) estimate genetic parameters for feed intake using the X-ray method in Atlantic salmon and 2) evaluate the ranking of Atlantic salmon families for the X-ray method against the gold standard family level intake in duplicate tanks for feed intake phenotypes.

## 2. Material and methods

In the present study, two parallel feed intake recording trials are described, the first is an individual-level X-ray trial recording feed intake for communally reared cohort and the second is a family tank-based feed intake recording trial on siblings from the same families. For the sake of brevity, commonalities between the two trials are described first followed by each specific trial described below.

### 2.1. Animal ethics statement

This study used measurements taken from a family experiment carried out at the Research Station for Sustainable Aquaculture (Nofima AS, Sunndalsøra, Norway). In strict compliance with the regulations for experiments on live animals in Norway (FOR-2015-06-18-761) and the EU (Directive 2010/637EU). The experiment was approved by the Norwegian Food Safety Authority (FOTS ID 23718).

### 2.2. Fish and husbandry

The fish used in the current trial were 35 full sibling families; i.e. the offspring of 35 single-pair mated sires and dams, from the breeding nucleus of MOWI Genetics AS (Øyerhamn, Norway). From fertilization, the 35 families were reared in separate trays, while from the eyed egg stage, the families were pooled and reared in a common garden tank. At an average body weight of 40 g, fish were PIT (Passive integrated transponder) tagged with (HPT12 12 mm, Biomark Ltd., Boise, USA, www.biomark.com) and genotyped using MOWI's customized SNP array which contains 55,735 single nucleotide polymorphisms (SNP) markers, which were used to assign the individuals to their families and to set up the genetic relationship (G) matrix (described below).

In August 2020 at an average body weight of 48.9 (SD = 7.9) grams, the fish were transported to the freshwater facility of Nofima Research Station for Sustainable Aquaculture, located at Sunndalsøra (62°40 N 8°31E), Norway. After a three-week acclimation period, the fish were sorted into two trials. For the gold standard tank trial 1750 parr from all the 35 families were distributed in two duplicate tanks per family (in total 70 tanks with 250 L water volume) and 25 fish per tank. The remaining 700 parr belonging to 34 of the 35 families were distributed into two rearing tanks (volume = 3.2 $m^3$, diameter = 2 m) with 350 fish per tank and from 5 to 15 fish per family per tank with a mean of 10. Both trials used the same water source and had a water temperature that varied from 11 to 13 °C. The dissolved oxygen ranged from 94 to 115%.

### 2.3. Feeds

Feed from a single feed mixture was used to produce to two feed sub-batches by extrusion (2.5 mm diameter pellets) using a Wenger TX-52 twin screw extruder (Wenger manufacturing INC. Sabetha, USA) Feed Technology Center (Nofima As, Bergen, Norway). The majority of the feed mixture was used to produce a sub-batch without any glass beads, while the last 50 kg of the feed mixture was supplemented with 3.0% glass beads radio-opaque markers (0.4–0.6 mm Ø) (Sigmund Lindner GmbH, Warmensteinach, Germany) to produce the second sub-batch (Difford et al., 2023). For the gold standard family tank trial the fish were fed the feed without beads for the entire trial. For the X-ray trial, the fish were also fed primarily the feed without beads but were fed the feed with beads the day preceding the X-ray imaging.

Across both the X-ray and the tank-based feeding trials very similar traits were recorded, however they can differ at the genetic level (individual or family) or time points. Trait abbreviations, definitions as well as the trial, the genetic level and the time of measurement are all summarised in Table 1 below.

### 2.4. X-ray feed intake and growth recording

The X-ray trial was conducted for 92 days from 15 September 2020 until 15 December 2020 as part of a longer ongoing growth trial, where the fish in the two tanks were X-rayed on days 22 (one of the tanks) and 23 (the other tank). During the first three weeks before the X-raying, the fish were gradually transitioned from continuous automated feeding to a feeding regime where they received the entire daily feed ration over 6 h (02:00–08:00). The day before X-ray, the fish were fed the feed with beads over the 6 h. After consuming the daily ration, fish were anesthetized, recorded for body weight ($BW_{Xi}$), and X-rayed over 5 h. For

**Table 1**
Definition of traits across trials.

| Abbreviation | Trait definition | Trial | Level | Time (days) | Units |
|---|---|---|---|---|---|
| $BW_{Xi}$ | Body weight | X-ray | Individual | 22 & 23 | g |
| $ADG_{Xi}$ | Average daily gain | X-ray | Individual | 22 & 23 | g/day |
| $DFI_{Xi}$ | Daily feed intake | X-ray | Individual | 22 & 23 | g/day |
| $DFI_{Xf}$ | Daily feed intake averaged per family per tank | X-ray | Family | 22 & 23 | g/day |
| $ADG_{Xf}$ | Average daily gain per family per tank | X-ray | Family | 22 & 23 | g/day |
| $ADG_{T}$ | Average daily gain per tank | Tank | Family | 49 | g/day |
| $DFI_{Tct}$ | Daily feed intake per fish in tank at common time as X-ray trial | Tank | Family | 22 & 23 | g/day |
| $DFI_{Tcw}$ | Daily feed intake per fish in tank trail at estimated common body weight as X-ray trial | Tank | Family | 22.6 ± 6 | g/day |
| $CFI_{T23}$ | Cumulative feed intake per tank | Tank | Family | 23 | g/day |
| $CFI_{T49}$ | Cumulative feed intake per tank | Tank | Family | 49 | g/day |

each fish average daily gain was calculated as the difference in body weight on day 22 (or 23) and day zero (15 September 2020) divided by the length of the growth period (i.e., 22 or 23 days) ($ADG_{Xi}$).

All X-rays were taken within the radiology unit at the Research Station for Sustainable Aquaculture, Nofima within a lead-shielded room. The X-ray source is an IMS Giotto mammography system (model number 6020/3, IMS Giotto, Bologna, Italy) equipped with a computer radiology system comprised of an FCR Profect image plate reader and FCR Console (Fuji Medical Inc., Japan). The X-ray source was set to 22 kVp / 50 mAs with a resolution of the system of 20 pixels/mm. The PIT tag was recorded and linked to the X-ray images for individual identification (Fig. 1). An image analysis program was used to count the beads within the gastrointestinal tract of each fish (Difford et al., 2023). A feed mass to bead number calibration standard series spanning 0.2 g to 2.2 g in increments of 0.2 g ($R^2 = 0.98$) was used to predict feed intake in grams per day (or the 6 h feeding period) for each individual ($DFI_{Xi}$) (Difford et al., 2023). The average daily feed intake per family (averaged per tank) was computed ($DFI_{Xf}$) for a comparison to the average daily feed intake per family (averaged per tank) from the family tank trial.

### 2.5. Family tank feed intake and growth recording

The family tank trial was conducted over 50 days from 15 September 2020 until 4 November 2020. Individual body weights of the 25 fish per tank were recorded at the start and the end of the trial with mean values of 50 g (SD = 8.2) and 110 g (SD = 22.6), respectively. The average daily gain was estimated as the difference in biomass per tank divided by the growth period ($ADG_T$). The families were fed the control feed at 15% of bodyweight in excess for the duration of the trial, the daily total ration was adjusted for each tank based on the amount of feed refusals (wasted) of the previous day. Feed was delivered by automated belt feeders, giving 7.2 × 15-s-long meals per hour (feeding every 500 s) throughout the 24 h. Daily records of feed offered, and uneaten waste feed collected in the feed spill were obtained for each of the 2 × 35 family tanks according to (Helland et al., 1996). A feed recovery test was done in each of the tanks before the start of the trial, using the same conditions (water flow, temperature, etc) as in the experiment, but without fish. There was a single mortality during the trial, the date of death and the weight of the fish were then used to adjust both the number and the fish biomass in the tank. Daily feed intake per family tank was computed as the difference in feed offered and uneaten wasted feed corrected for each tank's recovery rate and dry matter content of the uneaten feed. The average feed intake per individual fish in each family tank was calculated by dividing the daily feed intake of the family tank by the number of fish in the tank adjusted for mortalities ($DFI_T$). The average $DFI_T$ for days 22 and 23 was calculated to make a comparison with the X-ray feed intake trial on a common time basis ($DFI_{Tct}$). The fish in the family tank trial displayed an overall 11.1% lower growth rate (1.20 ± 0.23 $ADG_T$ over the 50-day growth period) than those in the X-ray trial (ADG 1.35 ± 0.19) over the 23-day growth period. As an additional quality control step, the average body weight per tank at the start of the trial and their respective average daily gain were used to interpolate the days at which the families in the tank trial would be at expected to be the same average body weight as their X-ray trial contemporaries on day 22 and 23. This was done to try to compare the daily feed intake of families in the tanks on a common weight basis ($DFI_{Tcw}$) and this was found to be at 22.6 days (SD = 6.0).

Lastly, the cumulative feed intake up until day 23 of the trial ($CFI_{T23}$) and day 49 (the last full day of feed intake recording) of the trial ($CFI_{T49}$) was computed to evaluate the relationship between the single snapshot measurement from the X-ray trial and the entire growth period in the family tanks.

### 2.6. Statistical analysis

#### 2.6.1. Individual-level genomic analysis of X-ray trial

Estimates of (co)variance components for the traits DFI, BW, and ADG were obtained from a tri-variate animal model using DMU version 6 (Madsen and Jensen, 2014):

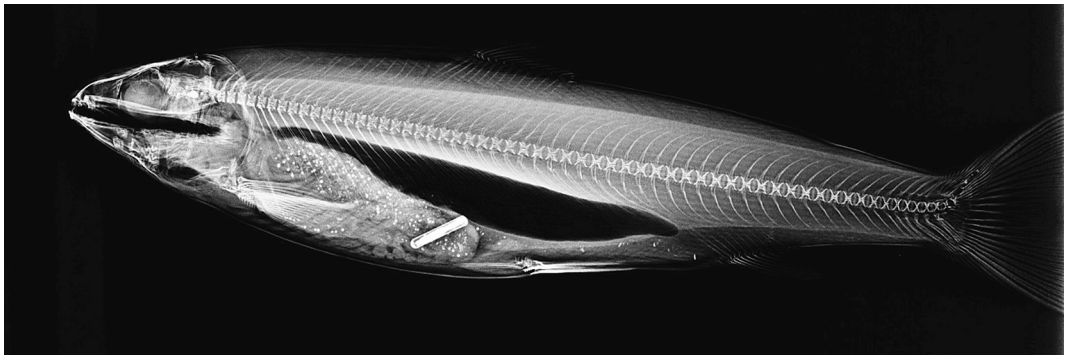

**Fig. 1.** X-ray image of an Atlantic salmon parr with radio-opaque beads inside the digestive tract (white spots) and the passive integrated transponder tag for individual identification.

$$\begin{bmatrix} \boldsymbol{DFI}_{Xi} \\ \boldsymbol{BW}_{Xi} \\ \boldsymbol{ADG}_{Xi} \end{bmatrix} = \boldsymbol{T}_i + \boldsymbol{S}_j + \boldsymbol{a}_k + \boldsymbol{e}_k \quad (1)$$

where $T_i$ is the fixed effect of the tank ($i = 1$ or 2), $S_j$ is the fixed effect of sex (j = 1 or 2), and $a_k$ is the random additive genetics effects with $a \sim$ ND (0, $\mathbf{G}\sigma^2_a$), where **G** is the genomic relationship matrix derived from the Van Raden method one (VanRaden, 2008) and $\sigma^2_a$ the additive genetic variance, and $e_k$ is the residual error e $\sim$ ND (0, $\mathbf{I}\sigma^2_e$) where **I** is an identity matrix and $\sigma^2_e$ the residual variance.

Heritability ($h^2$) was calculated as the ratio of additive genetic variance to total phenotypic variance $\sigma^2_a/(\sigma^2_a + \sigma^2_e)$. The genetic correlations ($r_g$) between pairs of traits were estimated as the genetic covariance divided by the square root of the product of two variances i.e. $r_g = (\sigma_{a12})/\sqrt{(\sigma^2_{a1} * \sigma^2_{a2})}$

*2.6.2. Family level analysis between X-ray and tank-based trials*

Estimates of (co)variance components for the family means of the traits DFI and ADG from the X-trial and DFI and ADG from the family trial were obtained from a four-trait family model using DMU version 6 (Madsen and Jensen, 2014):

$$\begin{bmatrix} \boldsymbol{Y}_T \\ \boldsymbol{ADG}_T \\ \boldsymbol{DFI}_{Xf} \\ \boldsymbol{ADG}_{Xf} \end{bmatrix} = \begin{bmatrix} R_i + f_j + e_{ijk} \\ T_i + f_j + e_{ijk} \end{bmatrix} \quad (2)$$

Where $Y_T$ is one of the following traits of interest ($DFI_{Tct}$, $DFI_{Tcw}$, $CFI_{T23}$, $CFI_{T49}$) and $ADG_T$ from the tank-based trial, for which $R_i$ is the fixed effect of the Room in which the tanks were located ($i = 1$ or 2), $f_i$ is the random effect of family (j = 1 to 35) with $f \sim$ ND (0, $\mathbf{A}½\sigma^2_a$), where **A** is the additive genetic relationship matrix and $\sigma^2_a$ the additive genetic variance, and $e_{ij}$ is the random residual error due to family within the tank (k = 1, 2) with e $\sim$ ND (0, $\mathbf{I}\sigma^2_e$) where **I** is an identity matrix and $\sigma^2_e$ is the residual variance. While for the two traits $DFI_{Xf}$ and $ADG_{Xf}$ of the X-ray trial, for which $T_i$ is the fixed effect of the tank (i = 1 or 2), $f_i$ is as for the tank-based trial except (j = 1 to 34), while $e_{ijk}$ is the random residual error for the traits in the X-trial. The proportion of variance explained by the family effect was calculated as the $h^2_f = \sigma^2_f/(\sigma^2_f + \sigma^2_e)$ where $\sigma^2_f$ is the family variance. As the fish in the X-trial and the family trial were different (although from the same families), the residual correlation was restricted to 0 assuming no residual covariances between the studies traits in the two trials. The between-family genetic correlation for pairs of traits was estimated as $r_f = (\sigma_{f12})/\sqrt{(\sigma^2_{f1} * \sigma^2_{f2})}$

## 3. Results and discussion

### 3.1. Daily feed intake from X-ray method and growth traits

There was no mortality during the X-ray recordings or in the following weeks after the X-ray. However, 2.1% ($n = 15$) of the recorded individuals had low-quality X-ray images because the fish moved while under anaesthetic and X-ray imaging. This resulted in partial doubling of beads in the X-ray image, thus the feed intake from these individuals was omitted from the data. In general, the feed intake during the 6 h feeding period was on average 0.96 g per fish but with substantial variation among individuals with CV = 27% (Table 1).

### 3.2. Genomic parameters of individual feed intake and growth traits from X-ray trial

The estimate of genomic heritability of daily feed intake ($h^2 = 0.19 \pm 0.06$) was significantly different from zero and of the same magnitude as the associated growth-related traits $BW_{Xi}$ and $ADG_{Xi}$ $h^2 = (0.20–0.24)$ (Table 2). Strong evidence of genetic variation in daily feed intake have also been reported in other farmed fish species: In rainbow trout (*Oncorhynchus mykiss*) X-ray imaged from 141 g to 2.167 kg, the estimated heritability of feed intake was 0.02–0.19 across normal and high protein diets (Kause et al., 2006a). In European white fish (*Coregonus lavaretus*) measured from 40 g – 131 g, heritability estimates were 0.17–0.23 (Quinton et al., 2007). Finally, in Chinook salmon (*Oncorhynchus tshawytscha*) from approximately 0.5 to 2 kg, Walker et al. (2012) estimated heritability for feed intake in the range of $h^2 = 0.29–0.39$. More recently, Scholtens et al. (2023) estimated heritability of feed intake in Chinook salmon 0.18–0.20 between 1 and 2 kgs. The referred to literature indicates that the heritability of DFI increased with body size, however, more comprehensive investigations are needed to confirm this. (See Table 3.)

**Table 2**
Descriptive statistics of feed intake and growth rate traits from the X-ray trial in Atlantic salmon.

| Traits | N | Mean | SD | Min | Max | CV % |
|---|---|---|---|---|---|---|
| $DFI_{Xi}$ | 685 | 0.96 | 0.27 | 0.2 | 1.8 | 27 |
| $BW_{Xi}$ | 700 | 80.0 | 13.6 | 40 | 121 | 17 |
| $ADG_{Xi}$ | 700 | 1.48 | 0.34 | 0.43 | 2.5 | 23 |

N = number of individuals, SD = standard deviation CV = coefficient of variation. Note subscripts X indicates X-ray trial on individual i. DFI = daily feed intake, BW = body weight, BL = body length, and ADG = average daily gain.

The genetic correlations between $DFI_{Xi}$ and associated growth-related traits were all positive and moderate with $BW_{Xi}$ (0.48) and strong (0.81) with $ADG_{Xi}$ (Table 2). Estimates of genetic correlations between $DFI_{Xi}$ with growth traits and other traits are scarce in the literature as most research has focussed on feed efficiency traits like FCR and RFI directly. However, the sign and magnitude of genetic correlations between growth traits and $DFI_{Xi}$ are in the range of literature estimates available. For example, body weight and DFI was genetically correlated at 0.73 in rainbow trout (Kause et al., 2006a) and 0.77 in Nile tilapia (*Oreochromis niloticus*) (de Verdal et al., 2018). Similarly, the genetic correlation between average daily gain and DFI was 0.93–0.97 in European whitefish (Quinton et al., 2007) and 0.62 in Nile tilapia (de Verdal et al., 2018). Positive genetic correlations between growth rate related traits and DFI are to be expected as increased growth requires more nutrients and the availability of nutrients is conditional on the gross daily feed intake as well as digestion, absorption, and energy partitioning (Knap and Kause, 2018). However, genetic correlations between growth and DFI approaching unity would indicate that there is no added benefit to recording DFI as all genetic variation is captured by growth. The genetic correlation between ADG and DFI (0.81) indicates approximately 66% of the genetic variation in DFI is explained by average daily gain. As can be seen from the genomic breeding values for DFI plotted against ADG (Fig. 2) there is variation in feed intake at any fixed point for ADG and *visa versa*. This suggests that recording DFI can provide information about feed efficiency over and above ADG and thus there is scope for additional genetic improvement in feed efficiency in Atlantic salmon through direct selection for feed efficiency.

**Table 3**
Estimates of variance components, heritability and genetic correlations for feed intake and growth rate traits from the X-ray trial in Atlantic salmon.

| Traits | N | $\sigma^2$a | $\sigma^2$e | $h^2 \pm$ SE | rg with $DFI_{xi}$ |
|---|---|---|---|---|---|
| $DFI_{Xi}$ | 685 | 0.014 | 0.057 | 0.19 ± 0.06 | N/A |
| $BW_{Xi}$ | 700 | 37.9 | 143.3 | 0.21 ± 0.06 | 0.64 ± 0.13 |
| $ADG_{Xi}$ | 700 | 0.023 | 0.089 | 0.20 ± 0.06 | 0.81 ± 0.09 |

N/A not applicable, N = number of individuals, $\sigma^2$a = additive genetic variance, $\sigma^2$e = residual variance, $h^2 \pm$ SE = heritability estimate ± Standard Error, Rg with $DFI_{xi}$ = genetic correlation with Daily Feed intake. Note subscripts X indicate X-ray trial on individual i. DFI = daily feed intake, BW = body weight, BL = body length, and ADG = average daily gain.

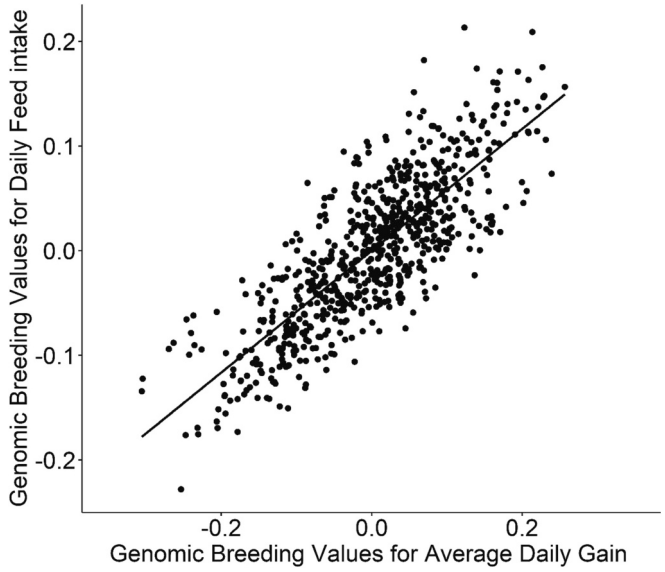


**Fig. 2.** Scatter plot of genomic breeding values for daily feed intake using the X-ray method in Atlantic salmon against their genomic breeding values for average daily gain.

### 3.3. Comparison of the X-ray method with tank-based feeding for feed intake at the family level

The average DFI of the X-ray trial was remarkably similar to that of the tank-based trial traits (Table 4).

The variation between families for the X-ray method was lower ($h^2f$ = 40%) than the daily feed intake at a common weight and common time in the tank trial which were both ($h^2f$ = 64%), respectively (Table 5). It is not completely clear why the between family variation for feed intake traits was markedly higher in the tank-based trial than in the X-ray trial, since the between family variance is lower for $DFI_{Xf}$ and residual variance is very similar for the two trials for feed intake traits (0.01–0.02). Thus, it is not likely due to increased error or noise in the X-ray phenotype, but could indicate that the X-ray method does not fully capture the between family variation for feed intake traits. However, the between family variation was also higher for $ADG_T$ (0.87 ± 0.04) as compared to $ADG_{Xf}$ (0.70 ± 0.09) and together this indicates that it is possible the tank-based feeding trial increases the between family variation. This could possibly be due to indirect genetic effects in the tank-based trial, where families which are genetically more or less cooperative through their social interactions inflate the differences in feed intake between the families. Whilst in the X-ray trial, communal rearing of many individuals and families in two tanks prevented potential social interactions partially confounding with between family genetics and diluted out the effects of social interactions.

Cumulative feed intake until the same time as the X-ray measurement in the siblings had higher between family variation ($h^2f$ = 0.75) than $DFI_{Xf}$ and this increased throughout the trial until the last full day of feeding to ($h^2f$ = 0.85) for $CFI_{T49}$. One possibility is that by specifically adjusting the daily feed intake of each family tank replicate based on their feed refusals, families are better able to express their genetic potential in the tank-based trial than in the X-ray trial where the feed offered is adjusted based on the combined requirements of all communal families in the tanks. This could mean that tank-based feeding constitutes a form of preferential environmental treatment or precision feeding which is partially confounded with genetic potential of families. More research is need to confirm this and ascertain to what extent this may deviate from commercial Atlantic salmon farming conditions.

Importantly our findings do still fall well within the broad range of family variation reported in smaller-scale studies conducted previously in Atlantic salmon family tank-based trials. For instance, Kolstad et al. (2004) studied feed efficiency 10 full sibling families until 28 g and found that the family accounted variation to be 77% in feed efficiency ratio. Whilst, Thodesen et al., (2001) looked at 14 full-sib families until 191 g and found that family accounted for 31% of the total variation in feed efficiency ratio and daily feed intake per unit body weight. Although neither of the above-mentioned studies estimated the family variation for daily feed intake, feed efficiency ratio does in part included daily feed intake in it's denominator and thus gives a likely lower limit to family variation in daily feed intake. More recently, Dvergedal et al. (2019) reported that family accounted for 92% of variation in cumulative feed intake in 23 full-sib families grown to 32 g. The broad range of estimates are likely due to differences in traits, number of families and the size and duration of fish.

The most important metric of comparison for the two trials is the genetic correlation between family breeding values ($r_f$) (Table 5, Fig. 2). Importantly, interpreting these correlations must be done with care as the standard errors of these estimates are large 0.18–0.19. Nonetheless, these estimates are worthy of consideration as to the best of our knowledge this is the only trial that has investigated family rankings between the two methods and is the largest family-based feed intake trial for Atlantic salmon. Encouragingly, the $r_f$ was strong and positive across all family tank-based feeding phenotypes with daily feed intake from the X-ray method. The highest correlation at ($r_f$ = 0.82) was for $DFI_{Tcw}$ (Fig. 3) and the lowest was at (Rf = 0.78) for $DFI_{Tct}$. Encouragingly, the family correlation between $DFI_{Xf}$ and all tank-based feed intake phenotypes was higher than with $ADG_T$ ($r_f$ = 0.70) further

**Table 4**
Descriptive statistics of family tank means of feed intake and growth traits from the X-ray trial and the tank-based trial in Atlantic salmon.

| Traits | N | Trial | Mean | Standard deviation | Min | Max |
|---|---|---|---|---|---|---|
| $DFI_{Xf}$ | 68 | X-ray | 0.96 | 0.13 | 0.64 | 1.3 |
| $ADG_{Xf}$ | 68 | X-ray | 1.35 | 0.19 | 0.72 | 1.8 |
| $DFI_{Tct}$ | 70 | Tank | 1.1 | 0.23 | 0.56 | 1.8 |
| $DFI_{Tcw}$ | 70 | Tank | 0.9 | 0.24 | 0.3 | 1.5 |
| $ADG_T$ | 70 | Tank | 1.20 | 0.22 | 0.55 | 1.7 |
| $CFI_{T23}$ | 70 | Tank | 17.3 | 3.2 | 8.8 | 24.6 |
| $CFI_{T49}$ | 70 | Tank | 45.5 | 7.3 | 24.7 | 59.5 |

N = number of families, SD = standard deviation, Traits = Average Daily Feed intake per family per tank in X-ray trial $DFI_{Xf}$, Average Daily Gain per family per tank in X-ray trial, Average Daily Feed intake per family in tank trial at a common time, Average Daily Feed intake per family in tank trial at common weight, Average daily gain per family in tank trial, Cumulative Feed intake per family until 23 days in tank trial, Cumulative Feed intake per family until day 49 of tank trial. Note subscripts X indicate X-ray trial on family f, T indicates tank-based trial at a common time (ct) or common weight (cw), 23 indicate day 23, and 49 indicates day 49 of the trial. ADG = average daily gain, DFI = daily feed intake, and CFI = cumulative feed intake.

**Table 5**
Variance components for between ($\sigma_f^2$) and within ($\sigma_e^2$) family and family heritability ($h_f^2$) for daily feed intake (DFI), cumulative feed intake (CFI) and average daily gain (ADG) and their genetic correlations ($r_f$) with daily feed intake in the X-ray trial for Atlantic salmon.

| Traits | Trial | $\sigma_f^2$ | $\sigma_e^2$ | $h_f^2$ ± SE | $r_f$ ± S.E. $DFI_{Xf}$ |
|---|---|---|---|---|---|
| $DFI_{Xf}$ | X-ray | 0.007 | 0.01 | 0.40 ± 0.15 | N/A |
| $ADG_{xf}$ | X-ray | 0.022 | 0.01 | 0.70 ± 0.09 | 0.89 ± 0.09 |
| $DFI_{Tct}$ | Tank | 0.03 | 0.02 | 0.64 ± 0.10 | 0.78 ± 0.19 |
| $DFI_{Tcw}$ | Tank | 0.03 | 0.02 | 0.64 ± 0.10 | 0.82 ± 0.19 |
| $ADG_T$ | Tank | 0.04 | 0.01 | 0.87 ± 0.04 | 0.70 ± 0.18 |
| $CFI_{T23}$ | Tank | 7.1 | 2.3 | 0.75 ± 0.08 | 0.82 ± 0.18 |
| $CFI_{T49}$ | Tank | 43.3 | 7.5 | 0.85 ± 0.01 | 0.73 ± 0.18 |

N/A not applicable, $r_f$ with $DFI_{xf}$ = genetic correlation with Daily Feed intake in the X-ray trial. Subscripts X indicate X-ray trial on family f, T indicates tank-based trial at a common time (ct) or common weight (cw), 23 indicates day 23, and 49 indicates day 49 of the trial.

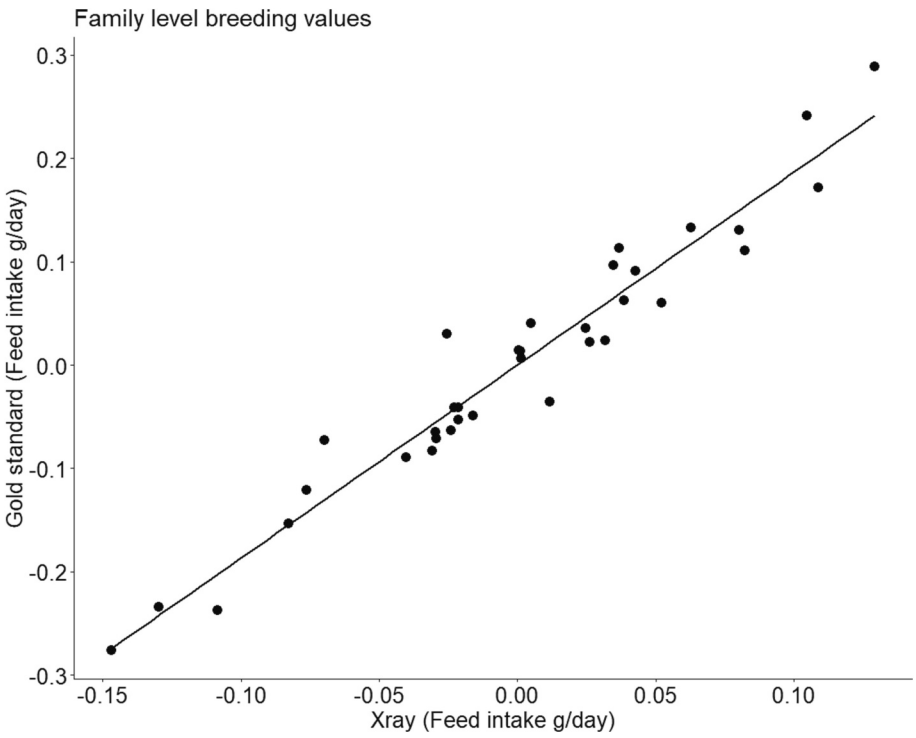


**Fig. 3.** Scatter plot of family breeding values for daily feed intake in Atlantic salmon using tank- based feed intake at a common weight of families against the X-ray method against their family breeding values for daily feed intake.

supporting the notion that feed intake records provide information over and above that of growth.

Since the correlation between family breeding values using the X-ray method offers a single snapshot in time, we compared this to the cumulative feed intake until day 23 and day 49 to get an indication of how representative a single snapshot measurement can be. The correlation between $DFI_{Xf}$ and $CFI_{T23}$ was strong and positive (rf = 0.82), however, the correlation dropped to 0.73 for $CFI_{49}$, indicating that a single snapshot measurement explains less and less variation in cumulative feed intake as the period over which cumulative feed intake is recorded increases. This finding is still encouraging as it demonstrates that the single daily measurement using the X-ray method is relevant to cumulative feed intake over short periods, in this case, 22–23 days but for longer growth periods more measurements are needed.

These findings confirm that a substantial proportion of the between-family genetic variation in the gold standard method is co-captured using the individual-level X-ray method. Although the correlation estimates are not significantly different from 1, this is due to the relatively high standard errors and less likely to be because the correlations are unity, as is evidenced by the consistent estimates around ~0.80. It is not clear what the precise causes are for the deviation from unity, but several factors could be contributing to this. By comparing families in two different tank environments, namely small family tanks in the tank trial and large mixed family tanks in the X-ray trial there could be genotype by environmental interactions occurring. For instance, the growth rate of the families in the tank-based trial was lower than in the X-ray trial (Table 4), despite steps taken to not disturb the families in the tank-based trial and minimize the disturbances caused by X-raying in the X-ray trial. Additionally, both trials were conducted on the same feed using the same water resources and the same water temperatures. To the best of our knowledge, no studies have attempted to genetically validate feed intake using the X-ray method. However, a study on Chinook salmon looked at the phenotypic correlation between the daily feed intake of 16 families with X-ray and the tank-based feed intake of the same 16 families and found a phenotypic correlation of 0.94 (Walker et al., 2012). In the comparison of Walker et al. (2012), there is no possible genotype by environmental interactions as both methods are recorded on the same individuals in the same tank environments. Future studies are needed to determine the extent to which family tank-based feed intake constitutes a different environment from a commercial setting, as this could call into question the relevance of this method as a gold standard in Atlantic salmon.

### 3.4. Future considerations for the X-ray method

The current study was conducted with relatively small fish on land during the freshwater life phase of Atlantic salmon growth. An important consideration is that the primary growth phase when Atlantic salmon go from 120 g smolt to 4–6 kg harvest-sized adults, occurs during the sea phase in commercial net pens. Studies in both Chinook salmon and rainbow trout have effectively handled larger specimens (>2 kg) with the X-ray method, but in both instances, this was conducted from tanks on land (Kause et al., 2006a; Walker et al., 2012; Scholtens et al., 2023).

Promising new portable digital X-ray detectors are available on the market and could potentially offer a cage-side solution to X-ray recording of individual feed intake of larger Atlantic salmon in the grow-out phase in net pens, however, at present studies testing this are lacking and needed. Future studies are also needed to test the feasibility of the X-ray method for obtaining feed intake records in large genetic cohorts of sea-phase Atlantic salmon and estimate genomic parameters.

Although this study demonstrated near equivalent ranking between a single X-ray feed intake record and the cumulative feed intake over 23 days, studies that investigate the temporal genetic variation over longer growth periods are needed to better identify the optimal number of feed intake recordings required to capture adequate genetic variation for cumulative feed intake. To this end, the herd-test day approach used in dairy cattle might prove effective, where cumulative 305-day yields in milk, fat, and protein production for individual animals are estimated using only 7–12 herd-test day measurements with random regression models and Legendre polynomials to predict breeding values for all 305 days in lactation and compute the cumulative 305-day breeding value

(Schaeffer et al., 2000). These models have been used for growth traits in turbot (*Scophthalmus maximus*) (Schlicht et al., 2018) and Nile tilapia (He et al., 2017; Rutten et al., 2005) but not for deriving cumulative breeding values or for feed intake traits. This would require multiple groups of fish recorded repeatedly for feed intake and growth traits on different days throughout the growth period. Another approach used in Nile tilapia is to record multiple meals over consecutive days and estimate the number of consecutive or random meal measurements needed to approximate the cumulative feed intake over the growth period (de Verdal et al., 2017).

Lastly, we found that growth rate did not explain all the genetic variation in daily feed intake and this is promising as it indicates genetic variation in feed efficiency. However, it remains to be seen whether there is any remaining unexplained genetic variation in DFI that is not explained by other energy sink traits (such as whole body lipid content) not only growth rate (Knap and Kause, 2018). If energy sink traits effectively explain all genetic variation in daily feed intake, it maybe possible to improve feed efficiency by properly weighting the energy sink traits in a selection index and circumvent the need for phenotyping of individual feed intake entirely. Future studies estimating the genetic parameters between energy sink traits and daily feed intake at different production life stages of Atlantic salmon production are sorely needed to answer these questions.

## 4. Conclusions

Recording daily feed intake in Atlantic salmon for breeding purposes using the X-ray method is feasible in parr. The genomic heritability estimates for daily feed intake was significantly heritable at 0.19 ± 0.06 and comparable in magnitude to those for growth traits. The correlation in family breeding values was consistent and high between the tank-based feeding of families and the X-ray method was 0.78–0.82, confirming a substantial between family genetic variation is captured by both methods with similar ranking.

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## CRediT authorship contribution statement

**G.F. Difford:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **B. Hatlen:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Writing – review & editing. **B. Gjerde:** Formal analysis, Methodology, Writing – review & editing. **K. Heia:** Methodology, Software, Writing – review & editing. **G. Baeverfjord:** Investigation, Methodology, Writing – review & editing. **A. Norris:** Data curation, Funding acquisition, Writing – review & editing. **A.K. Sonesson:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing.

## Declaration of competing interest

The authors declare that Dr. Ashie Norris is employed by MOWI Genetics ASA, while the other authors declare no conflicts of interest financial or otherwise.

## Data availability

Data will be made available on request.

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## References

Besson, M., Allal, F., Chatain, B., Vergnet, A., Clota, F., Vandeputte, M., 2019. Combining individual phenotypes of feed intake with genomic data to improve feed efficiency in sea bass. Front. Genet. 10, 1–14. https://doi.org/10.3389/fgene.2019.00219.

Besson, M., Rombout, N., Salou, G., Vergnet, A., Cariou, S., Haffray, P., Allal, F., Vandeputte, M., 2022. Potential for genomic selection on feed efficiency in gilthead sea bream ( *Sparus aurata* ), based on individual feed conversion ratio , carcass and lipid traits, 24. https://doi.org/10.1016/j.aqrep.2022.101132.

Dai, P., Kong, J., Meng, X., Luo, K., Lu, X., Chen, B., Cao, B., Luan, S., 2019. Genotype by environment interaction for feed efficiency trait of the juvenile Pacific white shrimp Litopenaeus vannamei held in individuals vs. in groups. Aquaculture 500, 506–513. https://doi.org/10.1016/j.aquaculture.2018.10.063.

de Verdal, H., Mekkawy, W., Lind, C.E., Vandeputte, M., Chatain, B., Benzie, J.A.H., 2017. Measuring individual feed efficiency and its correlations with performance traits in Nile tilapia, Oreochromis niloticus. Aquaculture 468, 489–495. https://doi.org/10.1016/j.aquaculture.2016.11.015.

de Verdal, H., Vandeputte, M., Mekkawy, W., Chatain, B., Benzie, J.A.H., 2018. Quantifying the genetic parameters of feed efficiency in juvenile Nile tilapia Oreochromis niloticus. BMC Genet. 19, 105. https://doi.org/10.1186/s12863-018-0691-y.

Difford, G.F., Hatlen, B., Heia, K., Bæverfjord, G., Eckel, B., Gannestad, K.H., Romarheim, O.H., Lindberg, S.K., Norris, A.T., Sonesson, A.K., Gjerde, B., 2023. Digital phenotyping of individual feed intake in Atlantic salmon (Salmo salar) with the X-ray method and image analysis. Front. Anim. Sci. 4, 1177396. https://doi.org/10.3389/fanim.2023.1177396.

Dvergedal, H., Ødegård, J., Øverland, M., Mydland, L.T., Klemetsdal, G., 2019. Selection for feed efficiency in Atlantic salmon using individual indicator traits based on stable isotope profiling. Genet. Sel. Evol. 51, 1–14. https://doi.org/10.1186/s12711-019-0455-9.

Dvergedal, H., Galloway, T., Sharma, S., Juarez, M., 2022. Verifying the Relationship between δ 13 C Isotope Profile Variables and Individual Feed Conversion Ratio in Large Rainbow Trout ( *Oncorhynchus mykiss* ) 558. https://doi.org/10.1016/j.aquaculture.2022.738355.

Falconer, D., Mackay, T., 1996. Introduction to Quantitative Genetics, Fourth, edi. ed. Longman Scientific and Technical, Harlow, Essex, United Kingdom.

Hatlen, B., Arnesen, A.M., Jobling, M., Siikavuopio, S., Bjerkeng, B., 1997. Carotenoid pigmentation in relation to feed intake, growth and social interactions in Arctic charr, Salvelinus alpinus (L.), from two anadromous strains. Aquac. Nutr. 3, 189–199. https://doi.org/10.1046/j.1365-2095.1997.00087.x.

He, J., Zhao, Y., Zhao, J., Gao, J., Han, D., Xu, P., Yang, R., 2017. Multivariate random regression analysis for body weight and main morphological traits in genetically improved farmed tilapia (Oreochromis niloticus). Genet. Sel. Evol. 49 (1), 1–13.

Helland, S.J., Grisdale-Helland, B., Nerland, S., 1996. A simple method for the measurement of daily feed intake of groups of fish in tanks. Aquaculture 139, 157–163. https://doi.org/10.1016/0044-8486(95)01145-5.

Henryon, M., Jokumsen, A., Berg, P., Lund, I., Pedersen, P.B., Olesen, N.J., Slierendrecht, W.J., 2002. Genetic variation for growth rate, feed conversion efficiency, and disease resistance exists within a farmed population of rainbow trout. Aquaculture 209, 59–76. https://doi.org/10.1016/S0044-8486(01)00729-3.

Iversen, A., Asche, F., Hermansen, Ø., Nystøyl, R., 2020. Production cost and competitiveness in major salmon farming countries 2003–2018. Aquaculture 522, 735089. https://doi.org/10.1016/j.aquaculture.2020.735089.

Jobling, M., Christiansen, J.S., Jørgensen, E.H., Arnesen, A.M., 1993. The application of x-radiography in feeding and growth studies with fish: a summary of experiments conducted on arctic charr. Rev. Fish. Sci. 1, 223–237. https://doi.org/10.1080/10641269309388543.

Kause, A., Tobin, D., Dobly, A., Houlihan, D., Martin, S., Mäntysaari, E.A., Ritola, O., Ruohonen, K., 2006a. Recording strategies and selection potential of feed intake measured using the X-ray method in rainbow trout. Genet. Sel. Evol. 38, 389–409. https://doi.org/10.1051/gse:2006011.

Kause, A., Tobin, D., Houlihan, D.F., Martin, S.A.M., Mäntysaari, E.A., Ritola, O., Ruohonen, K., 2006b. Feed efficiency of rainbow trout can be improved through selection: different genetic potential on alternative diets1. J. Anim. Sci. 84, 807–817. https://doi.org/10.2527/2006.844807x.

Kinghorn, B., 1983. Genetic variation in food conversion efficiency and growth in rainbow trout. Aquaculture 32, 141–155. https://doi.org/10.1016/0044-8486(83)90276-4.

Knap, P.W., Kause, A., 2018. Phenotyping for genetic improvement of feed efficiency in fish: lessons from pig breeding. Front. Genet. 9, 1–10. https://doi.org/10.3389/fgene.2018.00184.

Kolstad, K., Grisdale-Helland, B., Gjerde, B., 2004. Family differences in feed efficiency in Atlantic salmon (Salmo salar). Aquaculture 241, 169–177. https://doi.org/10.1016/j.aquaculture.2004.09.001.

Kolstad, K., Meuwissen, T.H.E., Gjerde, B., 2005. Efficient design for doing genetic studies of feed efficiency in Atlantic salmon (Salmo salar). Aquaculture 247, 153–158. https://doi.org/10.1016/j.aquaculture.2005.02.016.

Kolstad, K., Thorland, I., Refstie, T., Gjerde, B., 2006. Genetic variation and genotype by location interaction in body weight, spinal deformity and sexual maturity in Atlantic cod (Gadus morhua) reared at different locations off Norway. Aquaculture 259, 66–73. https://doi.org/10.1016/j.aquaculture.2005.12.022.

Madrid, J.A., Azzaydi, M., Zamora, S., Sánchez-Vázquez, F.J., 1997. Continuous recording of uneaten food pellets and demand-feeding activity: a new approach to studying feeding rhythms in fish. Physiol. Behav. 62, 689–695. https://doi.org/10.1016/S0031-9384(97)00155-8.

Madsen, P., Jensen, J., 2014. A user's guide to DMU, version 6, release 5.0. Center for Quantitative Genetics and Genomics Dept. of Molecular Biology and Genetics. University of Aarhus Research Centre Foulum. Box 50, 8830 Tjele Denmark.

Quinton, C.D., Kause, A., Ruohonen, K., Koskela, J., 2007. Genetic relationships of body composition and feed utilization traits in European whitefish (Coregonus lavaretus L.) and implications for selective breeding in fishmeal- and soybean meal-based diet environments. J. Anim. Sci. 85, 3198–3208. https://doi.org/10.2527/jas.2006-792.

Rodde, C., Vandeputte, M., Trinh, T.Q., Douchet, V., Canonne, M., Benzie, J.A.H., de Verdal, H., 2021. The effects of feed restriction and isolated or group rearing on the measurement of individual feed intake and estimation of feed conversion ratio in juvenile Nile Tilapia (Oreochromis niloticus) for selective breeding purposes. Front. Genet. 11, 1–11. https://doi.org/10.3389/fgene.2020.596521.

Rutten, M.J., Komen, H., Bovenhuis, H., 2005. Longitudinal genetic analysis of Nile tilapia (Oreochromis niloticus L.) body weight using a random regression model. Aquaculture 246 (1–4), 101–113.

Schaeffer, L.R., Jamrozik, J., Kistemaker, G.J., van Doormaal, B.J., 2000. Experience with a test-day model. J. Dairy Sci. 83, 1135–1144. https://doi.org/10.3168/jds.S0022-0302(00)74979-4.

Schlicht, K., Krattenmacher, N., Lugert, V., Schulz, C., Thaller, G., Tetens, J., 2018. Genetic analysis of production traits in turbot (Scophthalmus maximus) using random regression models based on molecular relatedness. J. Anim. Breed. Genet. 135 (4), 275–285.

Scholtens, M., Dodds, K., Walker, S., Clarke, S., Tate, M., Slattery, T., Preece, M., Arratia, L., Symonds, J., 2023. Opportunities for improving feed efficiency and spinal health in New Zealand farmed Chinook salmon (Oncorhynchus tshawytscha) using genomic information. Aquaculture 563, 738936.

Silverstein, J.T., 2006. Relationships among feed intake, feed efficiency, and growth in juvenile rainbow trout. N. Am. J. Aquac. 68, 168–175. https://doi.org/10.1577/a05-010.1.

Talbot, C., Higgins, P.J., 1983. A radiographic method for feeding studies on fish using metallic iron powder as a marker. J. Fish Biol. 23, 211–220. https://doi.org/10.1111/j.1095-8649.1983.tb02896.x.

Thodesen, J., Grisdale-Helland, B., Helland, S.J., Gjerde, B., 1999. Feed intake, growth and feed utilization of offspring Salmo, from wild and selected Atlantic salmon (Salmo salar). Aquaculture 180, 237–246.

Thodesen, J., Gjerde, B., Grisdale-Helland, B., Storebakken, T., 2001. Genetic variation in feed intake, growth and feed utilization in Atlantic salmon (Salmo salar). Aquaculture 194, 273–281. https://doi.org/10.1016/S0044-8486(00)00527-5.

VanRaden, P.M., 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91, 4414–4423. https://doi.org/10.3168/jds.2007-0980.

Walker, S.P., Ingram, M., Bailey, J., Dodds, K.G., Fisher, P.J., Amer, P.R., Symonds, J.E., 2012. Chinook salmon (Oncorhynchus tshawytscha) feed conversion efficiency : evaluation and potential for selection. Proc. N. Z. Soc. Anim. Prod. 72, 227–230.

Ziegler, F., Jafarzadeh, S., Skontorp Hognes, E., Winther, U., 2021. Greenhouse gas emissions of Norwegian seafoods: from comprehensive to simplified assessment. J. Ind. Ecol. 1–12 https://doi.org/10.1111/jiec.13150.