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Insights from the early generations of the Swedish rainbow trout (*Oncorhynchus mykiss*) breeding program

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ABSTRACT

This study aimed to gain insights about the status of the Swedish breeding program through studying key phenotypic traits. In total, 133 and 73 full-sib families were formed during the reproductive seasons of 2016 and 2019, respectively. Growth-related recordings were available from two occasions: ~ 9 and 24–27 months post-hatch. A preliminary descriptive analysis of the fecundity and early embryo survival identified substantial differences in favor of G0 (year class 2016) which was partly explained by the fact that first-time 3-year-old spawners were used in G1 (year class 2019). Moderate to high heritability values (0.23–0.49) were obtained for body length and weight across both time points and generations. Furthermore, the prediction accuracy of the estimated breeding values was ~0.65, while the expected genetic gain was 36 g per year. Overall, our results demonstrate the positive performance of the Swedish rainbow trout breeding program.

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KEYWORDS
Rainbow trout; selective breeding; BLUP; genetic parameter estimation

Introduction

Rainbow trout (*Oncorhynchus mykiss*) is one of the most domesticated and farmed aquaculture species worldwide (Teletchea & Fontaine, 2014). According to the Food and Agriculture Organization (FAO), the economic value of worldwide rainbow trout production in 2019 was approximately 4.155 billion US dollars. Notably, the typical harvest weight of rainbow trout varies widely from 200–250 g in Mediterranean to 400–600 g in the USA and up to 2 kg or more in Northern Europe. In Sweden, rainbow trout is the most popular farmed fish accounting for 40.2 million US dollars with a production volume of 10,400 t in 2021 (Jordbruksverket, 2022; SCB, 2023).

Selective breeding programs have played a pivotal role toward the expansion of the aquaculture industry (D'Agaro et al., 2021). Nowadays, more than 80% of the European finfish production originates from breeding programs, while the reported genetic gains for harvest weight ranges between 25 and 900% (Janssen et al., 2017). Currently, several breeding programs for rainbow trout operate worldwide (Boudry et al., 2021). A wide variety of traits have been targeted so far, including growth, fillet yield, fat content, age of sexual maturation and resistance to diseases (Gjedrem & Rye, 2016). Substantial genetic gains (>10%) per generation due to selective breeding schemes in rainbow trout have previously been reported for several traits like harvest weight and resistance to diseases (Gjedrem, 2005; Kause et al., 2005; Martinez et al., 2006a, 2006b; Leeds et al., 2016).

The driving force behind any breeding program is the maintenance of ample additive genetic variance. As such, mating schemes need to account not only for targeted trait values ofeach animal but also for the level of relationship between each breeding pair. Moreover, as farmed fish are characterized by high fecundity, solely focusing on improving the values of economically important traits can lead to a high inbreeding increase and potentially result in fitness reduction (Saura et al., 2017).

Therefore aquaculture breeding programs, like those in livestock or plants, rely on pedigree recordings for setting up appropriate mating pairs. Particularly in the case of salmonids like rainbow trout, nested mating designs are commonly applied where milt from one male fertilizes eggs from two or more females (Gjedrem & Baranski, 2009). This type of mating design aims to disentangle the additive genetic effect that is the underlying driving force behind genetic improvement from confounding factorslike maternal effects. Moreover,

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common practice involves rearing in separate incubation trays until hatching and later on in tanks for each individual family until a size suitable for marking with passive integrated transponders (PIT). Thereafter the animals are communally reared in order to minimize potential confounding environmental effects.

In general, family-based breeding programs comprised of a mixture of full- and paternal half-sibs are predominant in salmonid breeding programs (Chavanne et al., 2016). An additional advantage of the above design lies in the fact that it also allows for selection for traits where no phenotypic recordings are available for the breeding candidate per se as is the case with slaughter traits like fillet yield or ones related to disease resistance (Gjedrem, 2010). Nevertheless, unless genomic information is used, selection is possible only at the family level in that scenario. Not surprisingly, the use of a large number of families is critical for the long-term success and sustainability of a breeding program as otherwise inbreeding will accumulate rapidly. It is not uncommon nowadays to encounter salmonid breeding programs where more than 200 full-sib families are used (Gonen et al., 2015).

A rainbow trout breeding program was initiated in Sweden during the 1980s. The breeding strain originated from a Norwegian population that had undergone four generations of selection for increased growth rate and late sexual maturation (Donaldson & Olson, 1957; Sylvén & Elvingson, 1992). However, this first attempt was short-lived due to disease and funding issues. A new breeding program was initiated in 2011 using the remnants of the original strain in combination with broodstock from the Swedish rainbow trout industry.

A nested breeding design has been used in the Swedish breeding program where eggs from two females are separately fertilized by milt from one male. The first generation of the breeding program was established in 2016, and there are currently two generations of selectively bred rainbow trout. Compared to other salmonid breeding programs the Swedish one is relatively small with the first two generations comprised of 133 and 73 full-sib families, respectively (deviations from the expected 1 sire: 2 dam ratio are due to fertilization failure in certain matings). Best linear unbiased prediction (BLUP) is being used to estimate breeding values related to the growth potential of the farmed animals (Henderson, 1975), while at the same time, deformed animals or males showing signs of early sexual maturation (at the age of 1 year or earlier) are discarded.

Table 1. Number of crosses, sires, dams, and offspring recorded in two generations of rainbow trout (*Oncorhynchus mykiss*) selective breeding.

Generation	No. of crosses	No. of crosses with viable offspring	Sire	Dam	Offspring
G0	133	133	67	133	1768
G1	116	73	58	116	1643
Overall	249	206	125	249	3411

The objective of the current study was to evaluate the potential of further genetic improvement for growth traits in the Swedish rainbow trout breeding program, while at the same time gain also insights regarding reproductive traits like fecundity and embryo survival to the eyed stage. Genetic parameters for growth-related traits (measured on two occasions: ~9 and 24–27 months of age) were estimated based on records from two generations. Lastly, we assessed the prediction accuracy of the estimated breeding values and derived genetic gain expectations for body weight.

Material and methods

Breeding population

The rainbow trout breeding nucleus located at the facilities of Aquaculture Center North (ACN) in Kälarne, Sweden was the focus of our study. As mentioned before, the animals of each generation undergo selection for increased growth and against deformations or early sexual maturation in the case of males. A pedigree based BLUP is used to estimate breeding values of selected animals in the case of growth parameters. Overall, 67 sires (3–5 years of age) and 133 dams (4–5 years of age) were used to produce G0. To obtain G1, a total of 58 sires and 116 dams from only G0 (3 years of age) were used (Table 1). The selection intensity was 1.33 for males and 1.03 for females (Falconer & Mackay, 1996) with an overall average of 1.18.

Eggs from each individual cross were kept in separate incubating trays until hatching. Temperatures during the egg incubation to obtain G0 and G1 is presented in supplementary Figure 1. Unfertilized and dead eggs were removed from the trays to avoid spreading bacterial and fungal infections. Thereafter, fry from each full-sib family were transferred in separate 1 m^3 tanks until marking with PIT-tags at an average body weight of 60 g. Following tagging the family groups were mixed and reared together, initially in indoor tanks. Thereafter, from 16 months post-hatching they were reared in outdoor ponds.

Phenotypic trait recordings

Fecundity of each female ($n = 249$) used in the conducted crosses was estimated using the Brofeldt method (1935). More specifically, the number of eggs that fit within a 25 cm measuring trough were counted. In addition, the total egg volume was measured using a graded cylinder. The total number of eggs per female was then calculated by multiplying the above estimates. The relative fecundity for each female is presented as the number of eggs per kg body weight of the fish. Additionally, data for egg survival to the eyed stage were recorded on a family level for 249 unique matings. Fecundity and eyed stage egg survival records were available for both G0 and G1.

Growth traits (total body length and weight) were measured twice from each individual fish. The first measurements were taken during tagging at the age of ~ 9 months in both generations. The second recordings were measured at around 24 months post-hatch in G0, $n = 1768$, and 27 months post-hatch in G1, $n = 1643$, (Table 1). Phenotypic sex for both generations was recorded during the reproductive season when the animals were approximately three years of age. The sex of the fish was classified into three categories: males, females, or immature.

Descriptive statistics for each generation were computed for body weight, length, fecundity and egg survival to the eyed stage using statistical software packages in R (version 4.0.2).

Estimation of genetic parameters

Heritability estimates were obtained for the growth-related traits. Variance components were calculated using AIREMLF90 (Misztal et al., 2018). The following animal model was used:

$$y = Xb + Za + Tc + e \qquad (1)$$

where **y** is the vector of recorded phenotypes, **b** the vector of fixed effects. The fixed effects included age, sex and rearing pond. Significance of the above fixed effects was inferred through fitting a corresponding linear model (supplementary Table S1 and S2). **X** is the incidence matrix linking animal with fixed effects and **Z** is the incidence matrix linking animal with random effects. Moreover ***a*** is the vector of random animal effects $\sim N(0, \mathbf{A}\sigma_a^2)$, where **A** corresponds to the additive relationship matrix and σ_a^2 is the additive genetic variance. **T** stands for the incidence matrix linking animal with the common full-sib effect, whereas ***c*** $\sim N(0, \mathbf{I}\sigma_c^2)$ the vector of common random environmental effect due to the separate rearing of each individual full-sib family before tagging with σ_c^2 being the corresponding variance; ***e*** the vector of random residuals $\sim N(0, \mathbf{I}\sigma_e^2)$, where **I** the identity matrix and σ_e^2 the residual variance. Estimates of each variance component is represented in supplementary Table S3.

Heritability for growth traits was estimated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \sigma_e^2}$$

while the common full-sib effect was estimated as:

$$c^2 = \frac{\sigma_c^2}{\sigma_a^2 + \sigma_c^2 + \sigma_e^2}$$

The animal model **(1)** was used in two different scenarios: (i) the phenotypic data included recordings only from the parental generation (G0) or (ii) from progeny (G1).

Genetic correlations among growth traits

Genetic correlations among the growth traits (total length and weight) were estimated using a bivariate animal model including the same fixed and random effects as in (1). The model had the following format:

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_1 & 0 \\ 0 & \boldsymbol{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix}$$

where $\boldsymbol{y_i}$ are the vectors of the corresponding phenotypic traits under study; $\boldsymbol{b_i}, \boldsymbol{a_i} \sim N(0, \mathbf{G}_0 \otimes \mathbf{A})$ the vectors of fixed and random effects respectively and $\boldsymbol{e_i} \sim N(0, \mathbf{R}_0 \otimes \mathbf{I})$ the vector of residuals. $\mathbf{G}_0$ and $\mathbf{R}_0$ the 2×2 variance-covariance matrices for random effects and residuals, while $\otimes$ denotes the Kronecker product. $\mathbf{X_i}$ and $\mathbf{Z_i}$ the corresponding design matrices for the fixed and random effects.

The genetic correlations among traits was calculated using the following formula:

$$r_{i,j} = \frac{\sigma_{ai,aj}}{\sqrt{\sigma_{ai}^2 \times \sigma_{aj}^2}}$$

where $\sigma_{ai,aj}$ the genetic covariance between body traits, σ_{ai}^2 and σ_{aj}^2 are the corresponding additive genetic variances.

Estimation of breeding values

Estimated breeding values (EBVs) for the growth traits were calculated using the BLUPF90 software suite (Misztal et al., 2018). The breeding values were obtained from model (1) using phenotypic and pedigree data, which covered either G0 or G1 generation, or combined data across two generations (data presented in supplementary materials). Thereafter the breeding values were averaged per family and ranked from highest to lowest EBV.

In order to assess the accuracy of the conducted selection the average EBV of each mating pair from G0 was estimated and plotted against the mean phenotype of their respective progeny. The prediction accuracy (r) was approximated using predictf90 (Misztal et al., 2018) with the formula given below:

$$r = \frac{\text{correlation}(\mathbf{EBV}, \hat{Y})}{h}$$

where $\hat{\mathbf{y}}$ corresponds to the vector of phenotypes adjusted for fixed effects, **EBV** the vector of corresponding mid-parent breeding values and h is the square root of heritability.

Finaly, the expected genetic gain (ΔG) for increased body weight was computed using the breeder's equation (Falconer & Mackay, 1996):

$$\Delta G = \frac{r_{TI} \times i \times \sigma_\alpha}{L} \qquad (2)$$

where r_{TI} is selection accuracy, i is the selection intensity, σ_α the square root of additive genetic variance, and L is the generation interval in years.

Results

Descriptive analysis of phenotypic traits

Dams that were used to produce G0 had body weight ranging from 1016 g to 10,160 g (mean: 5882, SD 1551.5) and a total body length between 565 and 1100 mm (mean: 699, SD 61.2). The sires of the same generation had body weight ranging from 1842 g to 9920 g (mean: 5184, SD 1715.7) and total length between 509 and 830 mm (mean: 675, SD 68.6). In the case of G1, where all sires and dams were 3 years old, the dams had body weight ranging between 1810–4430 g (mean: 3196, SD 414.2) and a total body length between 525–630 mm (mean: 583, SD 22.6). The body weight and total length of the sires were 2337–3975 g (mean: 3196, SD 414.2) and 540–640 mm (mean: 592, SD 21.5), respectively (Figure 1).

The overall means for fecundity and egg survival showed substantial differences among the two year-classes (Figure 2). In particular, in G0 the mean fecundity was 6949 eggs/female (SD = 2119, range: 3665–17,491 eggs/female), while a mean value of 3831 eggs/female (SD = 1374, range: 1272–8802 eggs/female) was recorded in G1. In addition, the average relative fecundity in G0 was 1300.6 eggs/kg (SD = 890.7, range: 565.9–8659.5 eggs/kg), while the relative fecundity in G1 averaged at 1224.4 eggs/kg (SD = 447.9, range: 287.1–2653.6 eggs/kg).

Survival to the eyed stage for each mating pair varied widely (0–100%) across both year-classes with an average of 72%. More specifically, in G0, the survival rates ranged between 14% to almost 100%, while in G1 they varied from 0 to approximately 99%. Overall, the mean proportion of the eyed-stage survival was almost two times higher in G0 (an average of 90%) than in G1 (an average of 50%).

Moreover, growth-related parameters from G0 and G1 generations were recorded on two occasions. In the case of G0 the first-time measurement of body weight ranged from 25.7 g to 106.6 g, with a mean of 56 g (SD = 12.6), while the total body length varied between 125 and 196 mm, with a mean of 159 mm (SD = 11.4). The mean recorded weight during the second measurement was 835 g (SD = 196.3, range 186 g to 1334 g), while the mean body length was 399 mm (SD = 33.9, range 225 mm to 475 mm). Out of the 578 animals with recorded sex, 45% were males and 55% were females. Males had higher mean body weight and total length on both occasions. The average body weight was 5–9% higher, while the total length was 1–2% higher. During the second measurement, animals classified as immature had a lower body weight (2–4%) and length (5–13%) compared to mature ones (Table 2).

In the case of the early recordings for G1, the weight ranged from 19 g to 115 g with an average of 57 g (*SD* = 16.8), while the total length ranged from 117 mm to 201 mm, with an average of 161 mm (*SD* = 14.9). During the second measurement, the recorded body weights were between 219–2744 g with an average of 1779 g (*SD* = 328.8), whereas the range of length was between 360–565 mm with the mean at 495 mm (*SD* = 27.6) (Table 4). Among the 1171 animals with recorded sex, a balanced sex ratio was recorded. Males on average had 3–11% higher body weight and 1–2% higher length compared to females. The group of immature animals during the second measurement had 8–17% lower body weight and 1–3% lower length compared to the sexually mature animals (Table 3).

The phenotypic correlation among the recorded growth traits was significant ($P < 0.05$) within each time-point recording. A high phenotypic correlation was found between total length and body weight on both the first ($r = 0.95$) and the second recordings ($r = 0.89$) for G0 (Table 4). Similarly, a high correlation was found between body length and weight for G1 during the first and second measurements with correlation values of 0.95 and 0.85, respectively. On the other hand, a moderate correlation was found between the total length and body weight between first- and second-time measurements for G0 (0.31–0.35). While for G1 the respective correlation coefficients were 0.33–0.39 (Table 5).

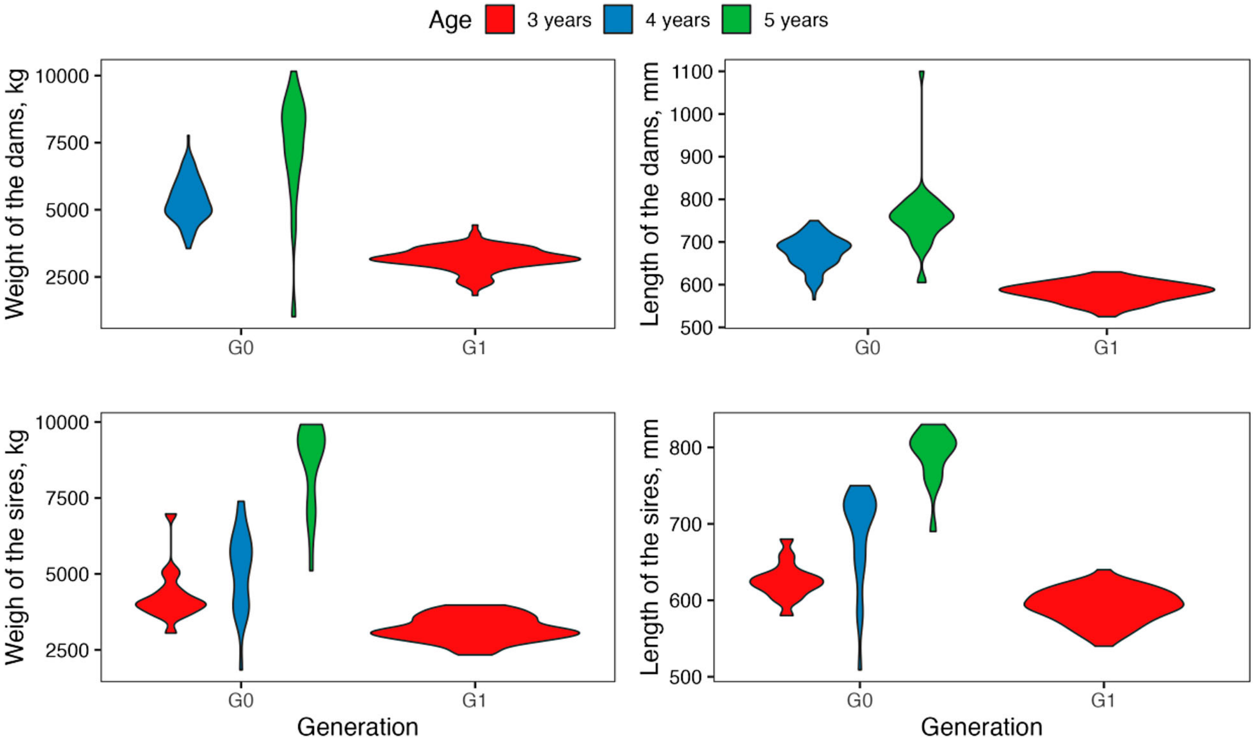

Figure 1. Body weight and total length for sires and dams used to produce the G0 and G1 generations of selectively bred rainbow trout (*Oncorhynchus mykiss*).

Estimates of genetic parameters

The heritability estimates of the recorded growth traits obtained when the two generations were analyzed independently varied from 0.32 (SE 0.15) to 0.49 (SE 0.27) in the first and from 0.23 (SE 0.11) to 0.37 (SE 0.12) in the second measurements (Table 4 and 5). When data from both generations were used (Table 6), heritability estimates were higher (0.37–0.48) with lower standard errors (0.05–0.06). The genetic correlations between body weight and total length measured in both generations were high and varied from 0.73 (SE 0.99) to 0.97 (SE 0.47) in both early and late recordings. While, amongst the early and late records, the genetic correlations were low to moderate and varied between 0.19 (SE 1.03) to0.48 (SE 0.38) (Tables 4 and 5). On both occasions though the estimated values were accompanied by substantially high standard errors.

Moreover, in G0, the full-sib effect (c^2) for early recordings was 0.12 (SE 0.06) and 0.11 (SE 0.07) for weight and length, respectively, while the corresponding values for late measurements were 0.02 (SE 0.04) for weight and 0.07 (SE 0.05) for length. In the case of G1, the common full-sib effect was 0.23 (SE 0.12) and 0.28 SE (0.12) for weight and length respectively during the first measurements, while in the case of the second measurement the values were 0.08 (SE 0.06) for weight and 0.15 (SE 0.07) for length.

Estimation of breeding values

Estimated breeding values were obtained through BLUP for the weight and total length. In the case of G0, the mean family EBVs ranged between −8.57 to 9.71 (weight) and −9.98 to 10.11 (length) for the first recordings. Whereas for the second recordings the mean family EBVs were between −250.78 to 181.21 for weight and −29.42 to 16.51 for length (Figure 3, supplementary Table S4).

The mean family EBVs of G1 during the first recordings ranged from −14.7 to 10.8 (weight) and from −8.69 to 8.65 (length). For the second recordings, the mean family EBVs ranged from −162.4 to 193.8 (weight) and from −14.66 to 13.4 (length) (Figure 4, supplementary Table S4).

Overall, a positive trend in EBVs for the later growth recordings was observed across families from the two generations. In particular, the mean estimated breeding value across all families in the former population (G0) was 0.09 and 1.38 for body length and weight, respectively. While in the selected population (G1), the respective values equaled 0.26 (body length) and 10.79 (body weight).

Furthermore, growth-related recordings (total length) from the latest generation (G1) were used to assess the prediction accuracy of the parental EBVs. In particular, the correlation coefficient among progeny phenotype

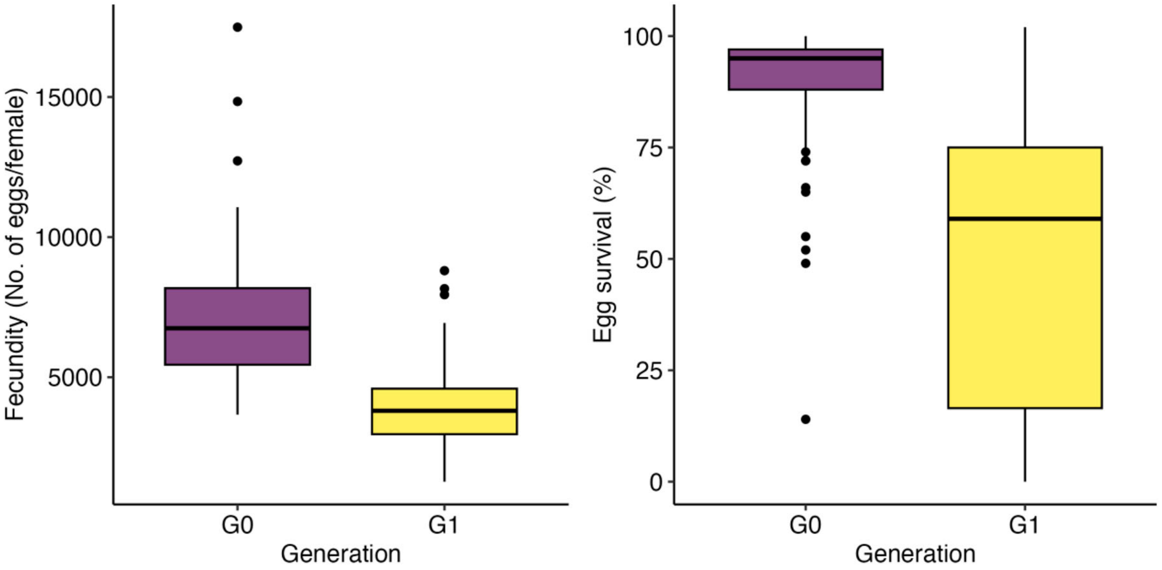

Figure 2. Proportions of eyed-stage survival in Swedish selectively bred rainbow trout (*Oncorhynchus mykiss*) families of G0 ($n = 133$) and G1 ($n = 116$).

(G1) and mid-parent EBV (G0) was 0.41 (supplementary Figure S2A) for the first and 0.31 (supplementary Figure S2B) for the second recordings. The accuracy of the estimated breeding values was equal to 0.66 (early measurements) and 0.65 (late measurements).

Genetic gain

To estimate the expected genetic gain the following information was used: the generation interval (3 years), an overall average selection intensity (1.18), and the prediction accuracy (0.65) for measurements taken on fish at the later life stage. At the same time an σ_α of 15.8 (body length) and 140.7 (body weight) was used respectively for each trait. Through the breeder's equation (2) the expected gain for body length and weight was 4 mm/year and 36 g/year respectively. Considering the estimates across all families as shown in the section above realized gains equaled to 0.1 mm/year for body length and 3.59 g/year for body weight (based on the dataset from G1 only); or 3.33 mm/year for body length and 16.82 g/year (based on combined dataset from G0 and G1, supplementary Table S5) were observed.

Table 2. Mean growth-related recordings per sex of selectively bred rainbow trout (*Oncorhynchus mykiss*) from parental generation (G0).

Sex	n	Weight 1st $^{(SD)}$ (g)	Weight 2nd $^{(SD)}$ (g)	Length 1st $^{(SD)}$ (mm)	Length 2nd $^{(SD)}$ (mm)
Male	258	$58^{(12.3)}$	$934^{(147.9)}$	$161^{(11.3)}$	$412^{(22.1)}$
Female	319	$55^{(12.9)}$	$852^{(143.3)}$	$159^{(11.3)}$	$403^{(22.6)}$
Immature	1191	$56^{(13.0)}$	$808^{(209.9)}$	$159^{(13.9)}$	$396^{(37.7)}$

n-number of animals, weight 1st and length 1st-weight and length at ~ 9 months of age, weight 2nd and length 2nd-weight and length at 24 months of age.

Discussion

Selectively bred rainbow trout from two subsequent year-classes were studied aiming to gain insights regarding the current status of the Swedish breeding program. In the case of reproductive traits, substantial differences in mean fecundity and survival to the eyed stage was observed between the two generations which was expected due to the age difference of the broodfish. Particularly, in G0 broodfish between 3 and 5 years were used, while in G1 all animals were of the same age (3 years).

Reproductive related traits are of critical importance for any aquaculture production system. Focusing on

Table 4. Heritability (diagonal), genetic (upper diagonal) and phenotypic correlations (below diagonal), and corresponding standard errors (superscripts) for growth traits in rainbow trout (*Oncorhynchus mykiss*) of parental generation (G0).

Trait	Length 1st (SE)	Weight 1st (SE)	Length 2nd (SE)	Weight 2nd (SE)
Length 1st (SE)	$\mathbf{0.39^{(0.16)}}$	$0.95^{(0.04)}$	$0.23^{(0.56)}$	$0.27^{(0.03)}$
Weight 1st (SE)	0.95	$\mathbf{0.32^{(0.15)}}$	$0.19^{(1.03)}$	$0.48^{(0.38)}$
Length 2nd (SE)	0.34	0.31	$\mathbf{0.23^{(0.11)}}$	$0.94^{(0.01)}$
Weight 2nd (SE)	0.34	0.35	0.94	$\mathbf{0.37^{(0.12)}}$

Weight 1st and length 1st-weight and length at ~ 9 months of age, weight 2nd and length 2nd-weight and length at 24 months of age. Phenotypic correlations were all statistically significant ($P < 0.01$).

Table 3. Mean growth-related recordings per sex of selectively bred rainbow trout (*Oncorhynchus mykiss*) of progeny (G1).

Sex	*n*	Weight 1st $^{(SD)}$ (g)	Weight 2nd $^{(SD)}$ (g)	Length 1st $^{(SD)}$ (mm)	Length 2nd $^{(SD)}$ (mm)
Male	583	59$^{(16.2)}$	1952$^{(323.9)}$	164$^{(14.1)}$	503$^{(27.5)}$
Female	588	57$^{(16.5)}$	1742$^{(291.5)}$	162$^{(14.9)}$	492$^{(26.3)}$
Immature	472	53$^{(16.9)}$	1611$^{(279.6)}$	158$^{(15.6)}$	487$^{(34.6)}$

n-number of animals, weight 1st and length 1st-weight and length at ~ 9 months of age, weight 2nd and length 2nd-weight and length at 27 months of age.

breeding programs, a decline in reproductive performance will most likely result in a rapid accumulation of inbreeding. The above will cause further deterioration that would eventually jeopardize the future of the breeding program. In our study, a substantial percentage of the set-up matings for G1 (~30%) did not produce viable offspring resulting in an almost 50% reduction in the number of obtained families compared to the one in the parental generation. The above could be explained to a certain aspect by the fact that in G1 all the female broodfish were first time spawners and therefore their reproductive performance was not at its peak (Mylonas et al., 2010). In addition, other external factors, e.g. temperature during egg incubation may have affected embryo development and survival rates (Weber et al., 2016). Notably, a temperature difference of 2–3°C was observed during egg incubation among the two generations (supplementary Figure S1).

Nevertheless, since we do not have a complete picture about the genetic diversity status of the base population of the Swedish rainbow trout breeding program we cannot exclude the possibility that the loss of such a high number of families as a result of poor fertilization and embryo survival was due to high inbreeding levels. Therefore, the usage of genomic technologies appears to be essential for elucidating the genetic diversity status of the breeding nucleus.

Table 5. Heritability (diagonal), genetic (upper diagonal) and phenotypic correlations (below diagonal), and corresponding standard errors (superscripts) for growth traits in rainbow trout (*Oncorhynchus mykiss*) of progeny (G1).

Trait	Length 1st $_{(SE)}$	Weight 1st $_{(SE)}$	Length 2nd $_{(SE)}$	Weight 2nd $_{(SE)}$
Length 1st $_{(SE)}$	**0.39$^{(0.26)}$**	0.97$^{(0.47)}$	0.44$^{(1.19)}$	0.35$^{(1.55)}$
Weight 1st $_{(SE)}$	0.95	**0.49$^{(0.27)}$**	0.33$^{(1.05)}$	0.44$^{(1.06)}$
Length 2nd $_{(SE)}$	0.38	0.33	**0.23$^{(0.17)}$**	0.73$^{(0.99)}$
Weight 2nd $_{(SE)}$	0.38	0.39	0.85	**0.28$^{(0.16)}$**

Weight 1st and length 1st- weight and length at ~ 9 months of age, weight 2nd and length 2nd-weight and length at 27 months of age. Phenotypic correlations were all statistically significant ($P < 0.01$).

Table 6. Heritability, genetic (upper diagonal) and phenotypic correlations (below diagonal), and corresponding standard errors (superscripts) for growth traits in rainbow trout (*Oncorhynchus mykiss*) of the combined data for parental generation (G0) and progeny (G1).

Trait	Length 1st $_{(SE)}$	Weight 1st $_{(SE)}$	Length 2nd $_{(SE)}$	Weight 2nd $_{(SE)}$
Length 1st $_{(SE)}$	**0.45 $^{(0.05)}$**	0.93$^{(0.02)}$	0.20$^{(0.11)}$	0.33$^{(0.11)}$
Weight 1st $_{(SE)}$	0.89	**0.46 $^{(0.05)}$**	0.13$^{(0.11)}$	0.35$^{(0.09)}$
Length 2nd $_{(SE)}$	0.23	0.20	**0.48$^{(0.06)}$**	0.84$^{(0.04)}$
Weight 2nd $_{(SE)}$	0.22	0.22	0.95	**0.37$^{(0.06)}$**

Weight 1st and length 1st-weight and length at ~9 months of age, weight 2nd and length 2nd-weight and length at 24 months of age. Phenotypic correlations were all statistically significant ($P < 0.01$).

Importantly, sexual growth dimorphism was observed even in early life stages. We found that amongst the fish with recorded sex in G0 ($n = 578$) and G1 ($n = 1171$), sexual growth dimorphism was observed well in advance of maturation (~9 months post-hatch). Males showed 5−11% higher mean body weight than females across two recordings. Evidence for sexual growth dimorphism was also shown on the Finnish rainbow trout breeding program with males having 2.3−14.4% higher body weight (Kause et al., 2003). This infers the importance of the inclusion of the phenotypic sex as an effect in the genetic model for estimating breeding values in the Swedish rainbow trout breeding program as otherwise the selected group of breeding candidates would be heavily skewed in favor of males. Molecular sexing approaches appear to be of value for early sex determination (Yano et al., 2013).

Phenotypic and genetic correlations amongst the growth-related traits

Our analysis revealed a significantly positive correlation between the recorded traits of the breeding population over two generations of selection. A positive phenotypic correlation among growth traits in fish species is common (Niva & Jokela, 2000; Rameez et al., 2020). Moreover, the correlation level between growth-related traits highly depends on the age of the animals under study. As such, the phenotypic correlations between early and late recordings of either weight or length were moderate (0.31−0.39).

Usually in salmonid breeding programs, the rearing conditions are not uniform in the early life stages amongst the entire population due to the fact that each family is kept in separate tanks until tagging. In our study, the first measurements were taken at ~ 9 months and the second at 24 months (G0) and 27

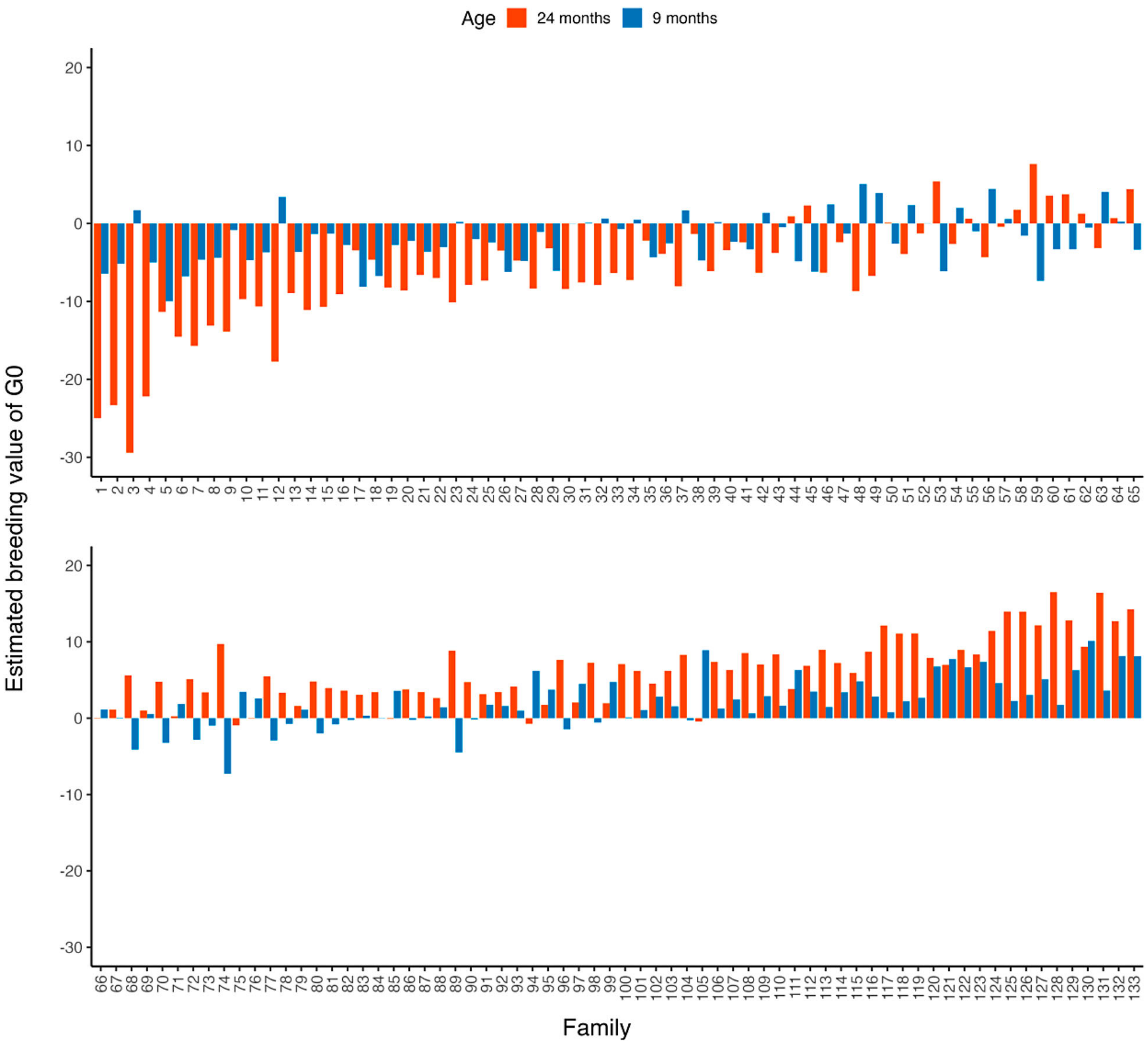

Figure 3. Estimated breeding values of each rainbow trout (*Oncorhynchus mykiss*) full-sib family from G0 based on body length measured at ~ 9 and 24 months of age.

months after hatching (G1). During the first recording, each family was kept at a separate tank, while on the second time point all families were communally reared in one (G1) or two ponds (G0). As such, the increase in the time between recordings led to the decreased phenotypic correlation amongst the first and second recordings. Possible explanations to this can be due to rearing each family in separate tanks until tagging size or due to genetic differences in the growth traits before tagging and at harvest as suggested by Le Rouzic et al. (2008). Therefore, an evaluation based on the earlier recordings may not lead to reliable breeding value estimates and animal ranking in the later life stages. The above is also supported by the low to moderate genetic correlations (0.19–0.48) between the growth-related traits of the first and second recording of both year-class. It should be stressed that even though the obtained genetic correlations of our study were accompanied by high standard errors, the range of the obtained values was in agreement with prior breeding studies in salmonids. In particular, similar results ($r = 0.47$) were reported for selectively bred Arctic charr of similar age interval, 9 and 24 months of age (Nilsson et al., 2016). In addition, a similar genetic correlation regarding body weight ($r = 0.35$) was also found in rainbow trout measured at 7- and 14-months post-hatching (Sae-Lim et al., 2013). Moreover, a decrease in genetic correlation estimates from 0.56 to 0.24 was reported by Su et al. (2002). for body weight measured on rainbow trout at 5 and 12 months of age. Overall, these findings highlight that animal re-ranking for growth traits may occur across different life stages.

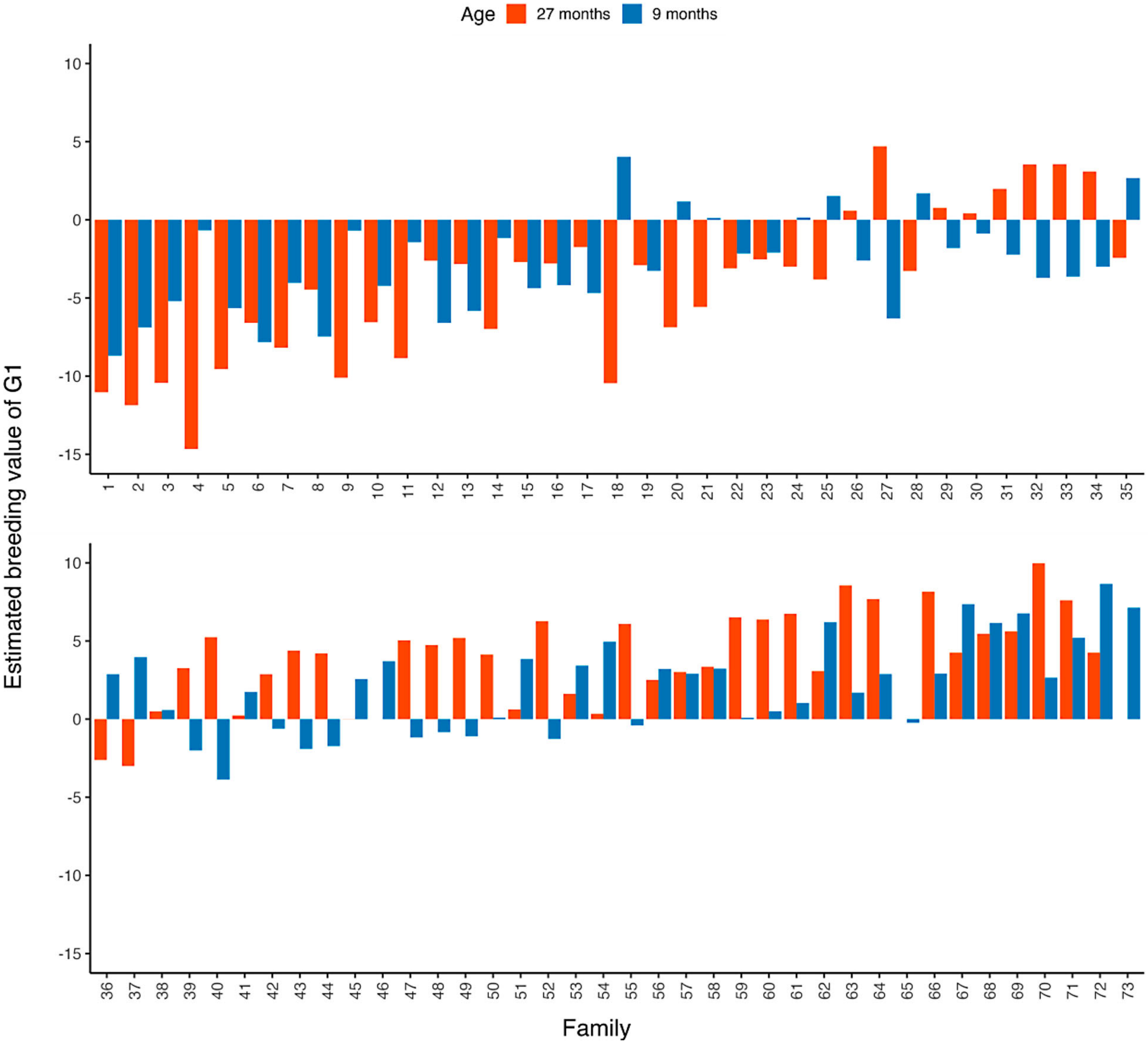

Figure 4. Estimated breeding values of each rainbow trout (*Oncorhynchus mykiss*) full-sib family from G1 based on body length measured at ~ 9 and 27 months of age.

Genetic parameters for growth-related traits

The present study estimated genetic parameters for growth-related traits (body weight and total length) at different ages (~9 and 24–27 months post-hatch). More specifically, heritability estimates were between 0.23 −0.49 for the two generations. As a benchmark, the magnitude of heritability values for growth traits reported in the literature for various life stages in salmonids varies widely from 0.09 to 0.60 (Sae-Lim et al., 2013; Tsai et al., 2015; Nilsson et al., 2016; Palaiokostas et al., 2021).

As already mentioned, differences in heritability estimates were observed in our study between the two recordings for both generations with generally higher values obtained during the first recordings. However, these values also had higher standard errors (SE = 0.15 −0.27), which could be mainly attributed to the existence of a shallow pedigree. Notably, the combined dataset produced higher heritability estimates (0.37 −0.48) and lower standard errors from 0.05 to 0.06 (Table 6) compared to the analysis on single generations. Another possible effect could be due to the confounding common full-sib effect as a result of rearing each family in different tanks until tagging (Gallardo et al., 2010; Haffray et al., 2012; Sae-Lim et al., 2013).

As expected, the magnitude of the common full-sib effect was also higher during the first recordings when the animals were ~ 9 months of age (0.11−0.28) compared to the recordings taken at 24−27 months of age (0.02−0.15) upon which point the animals were communally reared in ponds. A strong relationship between the common full-sib effect and life stage has been reported in the literature with the former usually reducing in later stages after rearing in a common environment with uniform conditions (Gallardo et al., 2010; Fu et al., 2016). Therefore, minimizing the time period before communal rearing is essential in order to minimize the common full-sib effect in family-based selective breeding.

Overall, the range of heritability estimates for body weight and length in the Swedish population of rainbow trout showed the existence of ample additive genetic variation for the growth traits. These results indicate a high potential for further genetic improvement through selective breeding practices.

EBV accuracy across generations – expected and realized genetic gain

The success of a breeding program can be monitored by the usage of progeny information for evaluating the accuracy of the parental generation EBVs. In our study, the accuracy of the parental generation EBVs (G0) was assessed based on the correlation between mid-parental EBV and the mean phenotypic value of their respective progeny. The obtained accuracy was 0.66 for the first time-point recordings and 0.65 for the second one, demonstrating a positive selection efficiency for improving growth traits in the rainbow trout breeding program. There are a few reports on the accuracy of BLUP-derived EBVs for growth-related traits in fish breeding schemes (Kause et al. 2005; Nielsen et al., 2009; Sae-Lim et al., 2017; Haffray et al., 2018). Nevertheless, we need also to account for the fact that the final recordings had a substantial time difference among the two generations which unavoidably adds substantial noise in the final estimates. However, the aforementioned is more likely to have resulted in a downward values of the estimated accuracy. Notably, our estimates were within the range of predictive abilities previously reported for such traits in salmonids with an intermediate heritability ($h^2 \approx 0.2-0.4$) that were shown to be 0.43–0.53 (Nielsen et al., 2009) and 0.72 (Haffray et al., 2018). While a lower accuracy was estimated by Sae-Lim et al. (2017) with the value of 0.37 when implementing traditional BLUP. Taking the above into account and in terms of future directions for the Swedish breeding program substantial improvements of the prediction accuracy for commercially important traits in rainbow trout have been documented through the usage of genomic information (Yoshida et al., 2018; Vallejo et al., 2020, 2021).

Importantly, the average EBVs of the formed families showed a general increase across the two generations. The expected genetic gain at the early generations of the Swedish rainbow trout breeding program was found to be 36 g/year in terms of body weight, while the realized gain equaled to 16.82 g/year (based on combined dataset from G0 and G1). However, as the base and selected populations on the second occasion were measured at the age of 24 and 27 months, respectively, the realized genetic progress should be considered as an approximation. Therefore more consistent recordings in the future will be essential for monitoring growth performance in the following generations and assessing the realized genetic gain of the traits under selection. Furthermore, since only 33% of animals of G0 reached maturation at three years of age genetic diversity could be depleted rapidly. Therefore it would worth to investigate the possibility of performing matings when the fish are four years of age. The latter could be beneficial toward retaining acceptable inbreeding rates (e.g. ∼ 1% per generation) in future generations (Bijma & Woolliams, 2000; Kause et al., 2005).

Conclusions

Our study documented for the first time genetic parameter estimates for growth-related traits and assessed the selection efficiency in the ongoing Swedish breeding program of rainbow trout. Moderate to high heritability estimates for growth-related traits were found, indicating that the Swedish rainbow trout breeding program has the potential to further enhance them in future generations. The estimated prediction accuracy from progeny testing further supports the above claim. Nevertheless, the substantial family loss due to poor fertilization and survival to the eyed stage is a source of concern that needs to be investigated thoroughly to assure the long-term sustainability of the breeding program. Finally, future usage of genomic information could elucidate the genetic diversity status of the breeding nucleus and potentially contribute toward further improving the prediction accuracy of the traits under selection.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Ethics approval

The study was conducted in accordance to Swedish legislation for conducting animal research as described in the Animal Welfare Act 2018:1192 (ethics permit: 5.2.18-09859/2019).

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