Maternal and genetic effects on embryonic survival from fertilization to swim up stage and reproductive success in a farmed rainbow trout line

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ABSTRACT

Reproductive success and offspring survival until sexual maturity are essential traits both for fish fitness and aquaculture development. Variation in offspring's survival among family results in unbalanced parental contributions to the next generation and may explain the loss of genetic diversity observed in some farmed populations. Therefore, we studied the variance in parental contributions to a progeny cohort, as well as the biological factors impacting offspring early survival in rainbow trout. The data consisted of 945 individual survival observations from fertilization to the juvenile stage from 135 full-sib families of the INRAE experimental synthetic line. Survival was assessed at eyed-egg stage, hatching, and 3 weeks after first feeding. We used a full-factorial mating design to partition phenotypic variance in early survival traits into maternal and additive genetic effects under threshold GBLUP models considering the inclusion of genomic information for 32,725 SNP. Average offspring survival proportions were 91.0% at the eyed-egg stage, 87.2% at hatching, and 84.4% three weeks after first feeding. Significant unbalanced dam contributions were observed at the eyed-egg and hatching stages. Low heritability was estimated for early survival traits (h^2=0.20 ± 0.12 and 0.13 ± 0.09 for survival from egg-eyed stage and, respectively, hatching and first feeding), revealing that additive genetic variance was not significantly different from zero, while maternal effects explained a larger part (c^2=0.37 ± 0.16 and 0.15 ± 0.07, respectively) of the phenotypic variances. There was no evidence of inbreeding depression on survival in our study. Phenotypically, offspring early survival was positively correlated with dam fecundity, while it was negatively correlated with dam post-spawning weight. Negative, but not significant association was observed between early survival and dam's average egg weight. If a study of genetic correlations confirms these phenotypic trends, promoting high fecund females should help the breeders to increase offspring early survival and to maintain genetic diversity in breeding programs.

1. Introduction

In animal breeding, there is a growing interest in selecting for robustness in farm species, as it allows promoting less-controlled and low-input systems where rearing conditions are more variable and unpredictable (Phocas et al., 2016). Survival in given environmental conditions is an ultimate robustness trait in fish breeding because it measures an individual's resistance to multiple mortality factors in a specific environment (Vehviläinen et al., 2008). In rainbow trout, little is precisely known about survival at embryo and larval stages, but juvenile fingerling survival is estimated at over 90% (Vehviläinen et al., 2010). Males are sexually mature at 1 or 2 years-old, while females attain maturity later at 2 or 3 years-old. In the wild, most fish only spawn once or twice in their lifetime (Christie et al., 2018), but females may reproduce once a year for 2 or 3 years in farming conditions. In good farming conditions, 2-year-old dams can produce 4700 eggs on average, corresponding to around 2300 eggs per kg of body weight (D'Ambrosio et al., 2020).

The contributions of genetic and maternal environmental effects to offspring survival can shift during development. Maternal components tend to be larger at early life (egg and alevin) stages because of the influence of maternal investment, such as egg quality, whereas additive

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genetic effects tend to be larger at later life (fry) stage, as shown in Atlantic salmon (Houde, 2015) and more generally in any animal species (Cheverud et al., 1983). Several studies in salmonids and carps have shown small sire effects but large dam effects on early survival (Herbinger et al., 1995; Fishback et al., 2002; Vandeputte et al., 2004; Houde et al., 2013). The genetic architecture of early survival traits was investigated under sire-dam genetic models in salmonids species (Kanis et al., 1976; Rye et al., 1990; Vehviläinen et al., 2012; Houde et al., 2015). All studies concluded that heritability of early survival was low to moderate, but impact of non-additive genetic factors and maternal environmental effects was important.

In fish breeding, high unbalanced progeny numbers between parents can be observed under mass spawning. Sperm competition under hatchery conditions using pools of sperm is a well-known phenomenon explaining unbalanced sire contributions in salmonids (Gharrett and Shirley, 1985; Gage et al., 2004) and carps (Kaspar et al., 2008). One of the consequences of the high variation in fish reproductive success and family size is the decrease in effective size and subsequent loss of genetic diversity in the next generation (Wedekind et al., 2007). Such phenomenon has been suggested as a likely factor to explain the observed loss of genetic diversity in a farmed rainbow trout line that was kept unselected since the early 1980 s (D'Ambrosio et al., 2019). In order to identify the key factors that may explain variance in reproductive success and thus loss of genetic diversity in a domesticated population of rainbow trout (*Oncorhynchus mykiss), w*e designed an experiment to determine maternal and genetic factors impacting offspring survival during embryonic and early larval development (from fertilization to three weeks after the first feeding). This topic has not been covered so much so far, and to our knowledge, studies were limited to small numbers of markers and did not partition maternal and genetic effects on embryonic and fry survival. Two main issues are raised in this paper: how do the early larval stages affect the variance in family size in farmed trout? What are the main genetic and maternal biological factors explaining variation in reproductive success and alevin survival in farm conditions?

2. Materials and methods

Experimentation was conducted at the INRAE experimental facility PEIMA (Sizun, France – Agreement number B29–277–02). The overall events of the experiment are presented in Fig. 1.

2.1. Population

The INRAE synthetic line was initially developed by inter-crossing several domesticated lines of rainbow trout to create a population with large genetic variability. The line was constituted from a mixture of French farmed populations with some new introductions from Denmark and the USA in the early 1980 s and then closed to outside germplasm (D'Ambrosio et al., 2019). Since then, the population has been maintained without intentional selection using a full factorial mating design between randomly chosen parents. About 60 dams and 80 sires were used at 2 years of age to produce each progeny cohort. An incident in the experimental facility led to the production of the 2019 study cohort from parents bred at 3 years of age.

2.2. Experimental mating design

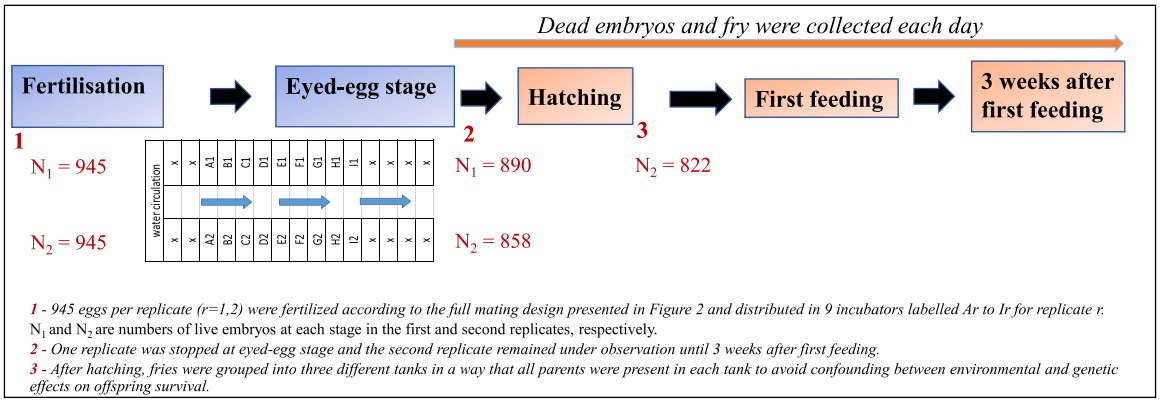
A full factorial mating plan was performed between 15 ovulated dams and 9 fluent sires of the INRAE rainbow trout synthetic line. The 3-year-old dams and sires were randomly divided into 3 groups of 5 females and 3 males, respectively. The groups of males were named Ma, Mb, and Mc, and males were labeled from 1 to 3 within their group name. In the same way, female groups were named Fa, Fb, and Fc, with a label from 1 to 5 for females within their group name. An ovulation checking was performed once a week, and brooders were maintained on average at 9 °C during the spawning season, to limit the occurrence of overripe eggs, as stated by Sakai et al. (1975) and Bry (1981).

In total, 945 ova per replicate were fertilized (Fig. 1) corresponding to 63 ova for each of the 15 dams. Nine aliquots of 7 ova were obtained from each female. The 35 ova from the 5 females of the same mating group were gently mixed before the fertilization process as routinely performed on the INRAE experimental facility. For each male, 1 mL of sperm was mixed with 1 mL of StorFish® (IMV, France), a dilution and preservation medium for salmonid milt. To avoid sperm competition (Pilastro et al., 2002; Wedell et al., 2002), the fertilization of 35 ova from each group of females (7 ova/female) was carried out male-by-male by adding 0.20 mL of sperm/StorFish mixture for each male (Fig. 2).

Each pool was then mixed with 15 mL of ActiFish solution (Supplementary Table A.1) to spread sperm over all the oocytes, and spring water was added 5 min later to activate oocyte fertilization. One hour after fertilization, all 105 eggs from a small factorial plan were grouped together in the same incubator until the eyed egg stage. The full mating design thus included 9 small factorial plans (each group of 5 females mated to each group of 3 males), generating 9 batches of 105 eggs placed in 9 egg incubators (named A to I) as described in Fig. 2. The 9 batches were duplicated to assess the consistency of the quantification of parental contributions at the progeny eyed egg stage. Incubators were positioned in the hatching trough as shown in Fig. 1 with duplicate batches facing each other.

2.3. Dam phenotypes

Dam phenotypes were measured on the day of spawning. Among the 17 females collected, two females were discarded due to the presence of



1 - 945 eggs per replicate (r=1,2) were fertilized according to the full mating design presented in Figure 2 and distributed in 9 incubators labelled Ar to Ir for replicate r.
N_1 and N_2 are numbers of live embryos at each stage in the first and second replicates, respectively.
2 - One replicate was stopped at eyed-egg stage and the second replicate remained under observation until 3 weeks after first feeding.
3 - After hatching, fries were grouped into three different tanks in a way that all parents were present in each tank to avoid confounding between environmental and genetic effects on offspring survival.

Fig. 1. Description of the experimental design.

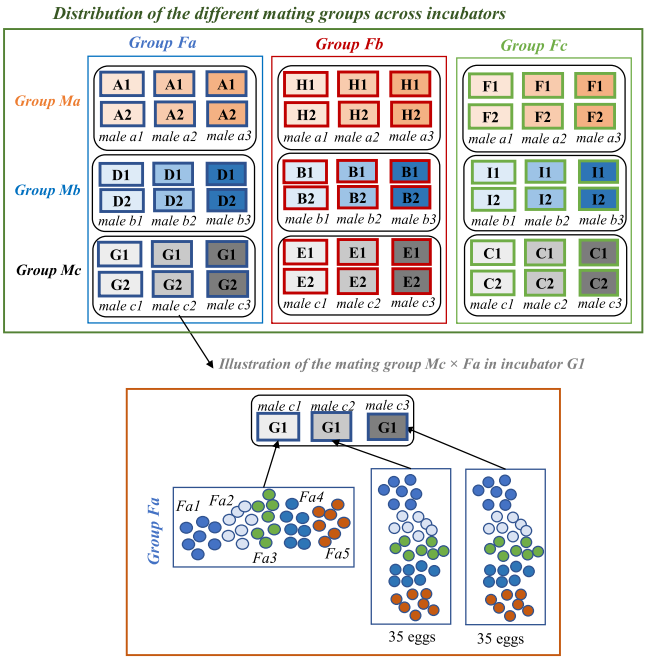


Fig. 2. Experimental mating design between the 3 male and 3 female groups and distribution of fertilized eggs in 2 × 9 incubators. Incubators A to I labelled " 1 " corresponded to the first replicate and incubators labelled " 2 " to the second replicate. In each incubator, fertilized eggs came from a specific mating design of one group of males and one group of females, as illustrated for incubator G1 where each male sperm from group Mc was crossed one-by-one with a pool of 35 eggs from Fa group (5 ×7eggs/female).

blood in the egg mass for the first one and of over-ripe eggs for the second one.

Female post-spawning weight (PW in g) and the fork length (FL in mm), spawn weight (SW) and the weight of the coelomic fluid (CF) were recorded. Two batches of 50 eggs were randomly collected from each egg mass to obtain the weight of 50 eggs and then, by dividing by 50, an average egg weight (EW) for each female. The ratio SW / EW allowed us to estimate the egg number in the spawn (EN). Then, the relative fecundity of each dam (RF) was calculated as EN/PW.

An additional 20 g sample of each egg mass was taken to get an accurate estimate of egg diameter (ED) and its coefficient of variation to assess spawn heterogeneity. To do so, a picture of the egg sample after 24 h of hydration in spring water was obtained using the *VisEgg* system (Cardona et al., 2020), a dedicated imaging system consisting of a light tablet and digital SLR camera (canon EOS 1000D, resolution: 10.1 M pixels). Each picture was analyzed with *Visilog 7.3* software (Thermo Scientific) to allow the automatic detection and measurement of each egg's diameter. In each 20 g sample of egg mass, there were, on average, 318 oocytes.

2.4. Offspring phenotypes

Standard husbandry practices were followed, with a daily bath with bronopol and daily dead eggs removal and counting. At the eyed egg stage, there were still 890 embryos in the first replicate and 858 in the second. All 890 embryos from the first duplicate of the experimental mating were sampled to be genotyped for parentage assignment. This first duplicate was only used to get the first estimate of parental contributions at the eyed egg stage. Due to the low number of eggs considered per mating pair, we were willing to assess the consistency of these early parental contributions by comparing estimates from two replicates. The second set of 858 embryos remained under observation from the eyed egg stage until the end of the experiment, three weeks after the first feeding (65 dpf at 12 °C). All dead fry were collected each day, and the presence of malformation (spine, head or caudal fin) was recorded. In addition, fry that did not complete yolk sac absorption were considered malformed. All fry (dead or alive) were sampled for genotyping.

2.5. Genotypes and parentage assignment

Genotyping was performed at the INRAE Gentyane Genotyping Platform (Clermont-Ferrand, France). The 890 offspring of the first replicate were genotyped for parentage assignment using 96 SNP in KASPar technology. Dynamic Array™ IFC 96 * 96 chips were used with Biomark™ HD Reader to perform the competitive PCR and chip reading. The Fluidigm® SNP Genotyping Analysis software was used to analyze the genotyping results. The panel of 96 SNP was chosen among the SNP from the Axiom™ Trout Genotyping array distributed throughout the whole genome and have a minor allele frequency (MAF) above 0.30 in the five French rainbow trout lines described in D'Ambrosio et al. (2019). This 96 SNP-panel is presented in Table A.2.

The 24 parents and the 858 offspring from the second replicate were genotyped for 57,501 SNP using the Axiom™ Trout Genotyping array (Palti et al., 2015). The quality control of genotyped SNP was performed as described by D'Ambrosio et al. (2019) to remove SNP with probe polymorphism and multiple locations on the trout genome. Only the 32,725 SNP with a call rate higher than 0.97, a test for the Hardy Weinberg equilibrium with a p-value > 0.0001, and a MAF higher than 0.05 were retained for further analysis. All missing genotypes for the 32,725 SNP were imputed using FImpute software with default parameters (Sargolzaei et al., 2014).

We used the R package *APIS* (Griot et al., 2020) to assign offspring of both replicates to their parents using a likelihood approach with decision rules based on the observed distributions of Mendelian transmission probabilities. We considered a maximum threshold of 1% for parentage assignment error.

2.6. Inbreeding coefficient and relatedness calculation

Runs of homozygosity (ROH) were identified for each fish using the PLINK v1.9 *homozyg* function (Chang et al., 2015), as defined by D'Ambrosio et al. (2019), with the following parameters: *'–homozyg-kb 1000 –homozyg -window-snp 30 –homozyg-snp 30 –homozyg-gap 1000 –homozyg-density 100 –homozyg-het 1'*.

The inbreeding coefficient (F_i) for any fish was calculated as the sum of ROH lengths ($\sum Length_{ROH,i}$) in this individual *i* divided by the total length of the autosomal genome covered by SNPs (*LGenome*): $F_i = \frac{\sum Length(ROH_i)}{LGenome}$.

The total size of the autosomal genome covered by SNPs (= 1874 Mb) was considered as the length of the genome, removing gaps of more than 1 Mb without any SNP from the total size.

Relatedness between pairs of parents was recovered using identity by descent (IBD) estimates from PLINK v1.9 software (*genome* function) (Purcell et al., 2007).

2.7. Statistical analyzes

Parental contributions were derived by counting each parent and pair's number of alive and dead progeny. With the help of R package *stats*, fisher exact tests were performed (*fisher.test* function) to assess potential unbalanced parental contributions to alive offspring at three stages: at the eyed egg stage for both replicates, at hatching, and 3 weeks after the first feeding for the second replicate. To control from multiple testing, the false discovery rate (FDR) method by Benjamini and Yekutieli (2001) was used to compare contributions two-by-two (*p.adjust* function).

In addition, offspring survival was evaluated from the day of fertilization to the time of the three stages for the second replicate: eyed egg

stage (Se), hatching (Sh), and 3 weeks after first feeding (Sf). Survival was also assessed between stages from eyed egg to hatching (Seh) and from hatching to 3 weeks after first feeding (Shf). Pearson correlations were computed between maternal phenotypes and offspring survival rates.

To assess the importance of genetic and maternal factors on early survival, we considered two phenotypes defined as binary traits: alive or dead from eyed-egg to hatching stages and from eyed-egg stage to three weeks after first feeding. From eyed-egg to hatching stages, 36 dead and 822 alive individuals were counted; 62 dead and 796 alive were counted from eyed-egg stage to the end of the experiment. The following genomic best unbiased prediction (GBLUP) models were considered to describe the vector of phenotypes (**y**) of the 858 offspring alive at the eyed-stage and genotyped with the 57 K chip.

Various genetic models (A- additive; AM- additive + maternal; AMD- additive + maternal dominance effects) were tested either considering (threshold model) or ignoring (linear model) the binary nature of the survival traits. The full tested GBLUP model described **y** under a linear (underlying) scale as: $y = X\beta + Za + Wd + Mc + bF_p + b_{sire} F_{sire} + b_{dam} F_{dam} + e$.

where **β, a, d, c** and **e** are the vectors of fixed incubator effects and random additive genetic effects, dominance deviation effects, maternal effects and residual effects, respectively. **X, Z, W** and **M** are the incidence matrices for **β, a, d** and **c**, respectively. The vectors **a** and **d** included the additive and dominance genetic values of the 858 individuals related through the genomic additive relationship matrix **G** and the dominance relationship matrix **D**. The **G** and **D** genomic matrices were built using the parallelef90 program (Vitezica et al., 2013).

The regression coefficients b, b_{dam}, b_{sire} on y of the vectors F_p, F_{dam}, F_{sire}, respectively, account for individual (progeny) and parental inbreeding effects on the studied performance.

Whatever the model, there were no significant effects of parental inbreeding levels. Therefore, these covariables were omitted in the final analysis. In addition, while the AMD linear model converged and gave the lowest AIC (Table A.4), the AMD threshold model did not converge to numerically consistent values.

Therefore, the final model retained as main result for the analysis and discussion of the results was: $\boldsymbol{y} = \boldsymbol{\beta} + \boldsymbol{Za} + \boldsymbol{Mc} + b\boldsymbol{F_p}$.

The two traits were analyzed separately using BLUPf90 package (Misztal et al., 2014) and the AIREMLF90 program (Thompson et al., 2005) for linear models or THRGIBBSF90 program (Tsuruta and Misztal, 2006) for threshold models. With the threshold model, the variance components were estimating using a Gibbs sampler with 200,000 cycles, 10,000 cycles of burn-in and 1 sample was kept every 40 cycles for posterior analysis. Convergence was checked by graphical inspection of both samples and posterior distributions of the parameters. All of these checks were implemented in POSTGIBBSf90 program (Aguilar et al., 2019).

3. Results

3.1. Genomic similarities among parents

The average inbreeding coefficients were close to each other for dams (12%) and sires (11%), with similar minimum values around 7% (Table 1). However, one dam had a very high inbreeding coefficient (28%) compared to all other parents (Fig. 3).

Table 1
Summary statistics of inbreeding coefficients for dams, sires and their progeny.

	F_{dam}	F_{sire}	F_p
Mean	0.121	0.110	0.102
SD	0.055	0.038	0.030
Minimum	0.071	0.066	0.003
Maximum	0.279	0.181	0.249

The majority of the parents were almost unrelated to each other (IBD $\leq$ 5% - Fig. 3). However, two pairs of parents were related with IBD values consistent with a half-sib relationship (ranging from 0.20 to 0.30).

On average, the inbreeding coefficient of the progeny was 0.10. Even for the two-parent pairs that were significantly related, the inbreeding coefficient of offspring was never extreme and did not exceed 0.25 (Table 1).

3.2. Offspring survival rates and parental contributions to the next generation

3.2.1. From fertilization to eyed egg stage (replicate 1 and 2)

From fertilization to the eyed egg stage, significant higher mortality was observed in the second replicate (R2), with 8.99% of dead offspring compared to 6.03% of dead offspring in the first replicate (R1). However, no significant (p-value > 0.05) interaction between parental origin and replicate was found for offspring survival (Fig. 4). Dams with a larger number of dead offspring in the first replicate generally also had a larger number of dead offspring in the second replicate.

In both replicates, disequilibrium in parental contribution, measured as alive eyed egg, was observed from fertilization to the eyed egg stage for dams but not for sires (Table 2).

3.2.2. From fertilization to three weeks after the first feeding (replicate 2)

In Tables 3 and 4, offspring survival rates at different stages in replicate 2 are presented. Offspring survival rate from fertilization to 3 weeks after the first feeding (Sf) varied from 63.5% to 95.2% among dams (Table 3) and from 78.1% to 91.4% among sires (Table 4). Larger differences in offspring survival were observed between dams (up to 33.3%-unit) than between sires (up to 13.3%-unit) at all stages. Statistically significant unbalanced contributions were only observed for dams (Table 3). Even if unbalanced dam contributions were seen on Sf, no significant dam effects were observed from hatching to three weeks after the first feeding (Shf). In addition, no significant effect of the dam-sire pairs was observed, but this can be due to the low number (7) of offspring per pair.

Fig. 5 shows the number of dead offspring from fertilization to eyed-egg stage, from eyed- egg stage to hatching and from hatching to three weeks after the first feeding for each dam or sire. Dams and sires were classified according to the number of their dead offspring at the end of the experiment, with the highest number of total dead offspring to the left and the lowest to the right. Three dams had significantly higher offspring mortality than the three best dams with the lowest numbers of dead offspring (Table A.3). No significant difference for the number of dead offspring was observed across sires. It appears that both paternal and maternal offspring survival were not significantly correlated between the different stages (Table 5).

3.3. Potential sources of imbalance in parental contributions

3.3.1. Quantification of genetic and maternal effects on offspring survival

Early survival variables had low heritability values of 0.196 for Seh and 0.134 for Sef under threshold models. Those values that were not statistically different from zero (Table 6). Slightly higher proportions of phenotypic variance were explained by the common maternal effects (including both genetic and environmental factors) estimated at 0.368 and 0.147, respectively for Seh and Sef (Table 6).

Under linear AM models (Table A.4), early survival variables had very low heritability values of 0.015 and 0.012, respectively for survival from eyed-egg stage to hatching stage and to the end of the experiment. Those values were lower values than those estimated under threshold model and transformed to the observed scale by Dempster and Lerner (1950) formula (0.035 and 0.042 for Seh and Sef, respectively). However in any of the alternative (observed or underlying) worlds, there was not significant additive genetic variance on early survival traits.

	Fa1	Fa2	Fa3	Fa4	Fa5	Fb1	Fb2	Fb3	Fb4	Fb5	Fc1	Fc2	Fc3	Fc4	Fc5	Ma1	Ma2	Ma3	Mb1	Mb2	Mb3	Mc1	Mc2	Mc3
Fa1	0,09	0.00	0.03	0.02	0.00	0.1	0.00	0.00	0.00	0.05	0.08	0.00	0.06	0.11	0.00	0.00	0.00	0.02	0.00	0.00	0.08	0.07	0.00	0.00
Fa2	0.13	0.00	0.09	0.00	0.09	0.00	0.00	0.00	0.06	0.09	0.12	0.13	0.04	0.00	0.00	0.00	0.00	0.00	0.04	0.12	0.04	0.00	0.00	0.00
Fa3	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Fa4	0.07	0.03	0.14	0.13	0.09	0.13	0.03	0.08	0.09	0.13	0.12	0.1	0.08	0.00	0.12	0.1	0.08	0.1	0.04	0.00	0.11			
Fa5	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	
Fb1	0.09	0.05	0.07	0.08	0.09	0.1	0.06	0.04	0.09	0.00	0.00	0.00	0.1	0.09	0.13	0.01	0.06	0.00	0.03					
Fb2	0.08	0.07	0.09	0.00	0.06	0.08	0.03	0.00	0.03	0.08	0.03	0.11	0.09	0.06	0.07	0.05	0.00	0.04						
Fb3	0.12	0.09	0.00	0.05	0.03	0.04	0.00	0.04	0.04	0.00	0.03	0.00	0.12	0.07	0.07	0.00	0.00							
Fb4	0.07	0.00	0.1	0.21	0.1	0.00	0.1	0.09	0.00	0.00	0.11	0.09	0.06	0.00	0.02	0.00	0.12							
Fb5	0.14	0.28	0.14	0.00	0.13	0.00	0.00	0.08	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00								
Fc1	0.1	0.14	0.12	0.15	0.07	0.00	0.27	0.11	0.03	0.08	0.06	0.05	0.00	0.03										
Fc2	0.09	0.03	0.09	0.1	0.14	0.00	0.09	0.02	0.12	0.00	0.06	0.00	0.08											
Fc3	0.09	0.12	0.05	0.00	0.00	0.00	0.05	0.04	0.07	0.27	0.07	0.00	0.05											
Fc4	0.12	0.00	0.00	0.00	0.00	0.08	0.07	0.13	0.07	0.00	0.00													
Fc5	0.12	0.1	0.00	0.05	0.00	0.06	0.00	0.00	0.00	0.08														
Ma1	0.15	0.00	0.08	0.05	0.05	0.00	0.00	0.00	0.06															
Ma2	0.16	0.04	0.00	0.00	0.00	0.00	0.00	0.00																
Ma3	0.08	0.12	0.09	0.08	0.15	0.00	0.04																	
Mb1	0.09	0.00	0.04	0.05	0.00	0.15																		
Mb2	0.09	0.00	0.00	0.00	0.08																			
Mb3	0.07	0.27	0.00	0.00																				
Mc1	0.08	0.00	0.00																					
Mc2	0.18	0.00																						
Mc3	0.11																							

Fig. 3. Inbreeding coefficients (diagonal terms) and identical-by-descent (IBD) values (upper triangular matrix) among all parents.

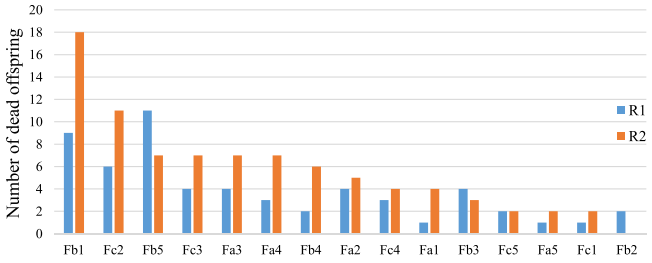


Fig. 4. Number of dead offspring per dam in both replicates (R1 and R2) from fertilization to eyed-egg stage.

Table 2
Fisher exact test for offspring survival per dam and sire from fertilization to eyed egg (Se), and for both replicates.

	Replicate 1		Replicate 2	
	Dams	Sires	Dams	Sires
Mean survival (Se)	94.0%	94.0%	91.0%	91.0%
SD	4.7%	3.4%	7.0%	3.7%
Minimum	82.5%	86.7%	71.4%	83.8%
Maximum	98.4%	98.1%	100.0%	95.2%
p-value	0.0059 *	0.0812	0.0005 *	0.1224

Proportions of phenotypic variance explained by the maternal effects were estimated at significant values, 5.8% and 3.4% under linear models for Seh and Sef, respectively. Those values were quite consistent with values estimated under threshold model and transformed to the observed scale by Dempster and Lerner (1950) formula (0.066 and 0.046 for Seh and Sef, respectively).

There was no significant association between early survival traits and neither parental inbreeding coefficients (Table A.5) nor offspring

Table 3
Statistics of progeny survival (Replicate 2) per dam at different stages and associated Fisher exact tests of dam differences in the numbers of dead and alive offspring.

	Mean	SD	Minimum	Maximum	P-value
Se	91.0%	7.0%	71.4%	100%	0.0005
Sh	87.2%	9.7%	65.1%	98.4%	0.0005
Sf	84.4%	9.3%	63.5%	95.2%	0.0005
Seh	95.6%	5.2%	82.1%	100%	0.0005
Shf	96.9%	2.7%	92.3%	100%	0.2364

Se: survival from fertilization to eyed-egg stage; Sh: survival from fertilization to hatching; Sf: survival from fertilization to 3 weeks after first feeding; Seh: survival from eyed-egg to hatching; Shf: survival from hatching to 3 weeks after first feeding

Table 4
Statistics of progeny survival (Replicate 2) per sire at different stages and associated Fisher exact tests of sire differences in the numbers of dead and alive offspring.

	Mean	SD	Minimum	Maximum	p-value
Se	91.0%	3.7%	83.8%	95.2%	0.1224
Sh	87.2%	3.9%	81.9%	93.3%	0.1559
Sf	84.4%	4.6%	78.1%	91.4%	0.1044
Seh	95.8%	2.5%	91.8%	99.0%	0.1584
Shf	96.8%	1.9%	93.3%	100.0%	0.3323

Se: survival from fertilization to eyed-egg stage; Sh: survival from fertilization to hatching; Sf: survival from fertilization to 3 weeks after first feeding; Seh: survival from eyed-egg to hatching; Shf: survival from hatching to 3 weeks after first feeding

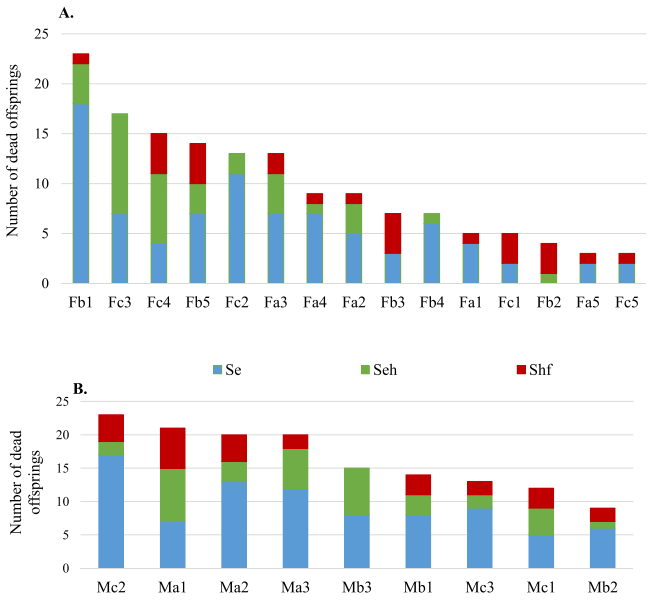


Fig. 5. Number of dead offspring (bar plot) from fertilization to eyed-egg stage, from eyed- egg stage to hatching and from hatching to three weeks after first feeding, for dams (A) and sires (B).

Table 5
Correlations between progeny survival rates at different stages (across dams in the upper triangular matrix and across sires in the lower triangular matrix).

	Se	Sh	Sf	Seh	Shf
Se	1	0.89*	0.84*	0.43	-0.27
Sh	0.81*	1	0.97*	0.79*	-0.18
Sf	0.76*	0.94*	1	0.80*	0.06
Seh	-0.15	0.45	0.42	1	-0.01
Shf	0.24	0.29	0.60	0.10	1

* significant correlation (p-value < 0.05).

Table 6
Additive genetic, maternal, and residual variances (σ_a^2, σ_m^2, σ_r^2), corresponding heritability (h^2) and proportion of phenotypic variance explained by maternal effects (c^2) were estimated under threshold GBLUP models. Standard errors of estimates are given in brackets.

Survival	Seh	Sef
σ_a^2	0.452 (0.332)	0.188 (0.150)
σ_m^2	0.849 (0.759)	0.207 (0.182)
σ_r^2	1.008 (0.090)	1.010 (0.097)
h^2	0.196 (0.116)	0.134 (0.087)
c^2	0.368 (0.156)	0.147 (0.075)

Source:Sources of variation of survival from eyed-egg stage until hatching (Seh) or 3 weeks after first feeding (Sef.

inbreeding (Table A.6).

3.3.2. *Maternal phenotypes and their associations with offspring survival rates*

Regarding female traits, two size and six reproduction traits were measured, and basic statistics are presented in Table 7. As expected from mathematical constraints for CV (Lande, 1977), the CV of the average egg weight (corresponding to a volume record) was roughly 3 times larger than the CV of egg diameter (corresponding to a length record). However, CV of both egg size traits were low (CV $< 10\%$). Concerning the three other reproductive traits (CF, EN, and SW) and the PW, there were variables between dams with CV of around 20%.

In addition, a phenotypic correlation between FL and PW was

Table 7
Summary of size and reproduction traits of the 15 dams at 3 years of age.

	Mean	SD	Minimum	Maximum	Coefficient of variation (%)
Fork length (FL, mm)	488	24.9	437	522	5.10
Post-spawning weight (PW, g)	2053	342	1382	2753	16.65
Spawn weight (SW, g)	267	55.4	178	406	20.73
Egg number (EN, #)	3765	831	2670	5908	22.06
Relative fecundity (RF, egg number/kg)	1.87	0.45	0.99	2.67	23.88
Weight of Coelomic fluid (CF, g)	27.8	5.2	19.2	35.2	18.55
Egg weight (EW, mg)	71.3	5.1	63.3	80.4	7.15
Egg diameter (ED, mm)	5.34	0.12	5.11	5.52	2.34

estimated at 0.69; EW and ED at 0.91; SW and EN at 0.95. The reproductive traits SW, ED and EW were positively correlated with FL or PW (Table 8). Negative but non-significant trends were generally observed for correlations between F_{dam} and maternal traits.

A graphical observation was first performed to ensure that the relationships between dam performances and progeny survival traits were globally linear before calculating the correlations between them.

Correlations of dam phenotypes with their progeny survival are presented in Table 9. Fork length was almost uncorrelated with survival until hatching, while PW was significantly and negatively correlated with survival until the hatching stage. After hatching, correlations between size traits and survival became weakly favorable. Note that the phenotypic correlation between average EW and ED was 0.91. Fecundity traits EN and SW were positively correlated with fry survival traits until hatching but almost uncorrelated with survival from hatching to 3 weeks after the first meal. Weak correlations that were not statistically different from zero were observed between all early survival traits and CF, EW, or ED. However it should be noted that offspring mortality observed from the eyed egg stage to hatching was significantly (p-value=0.003) higher in the dam group with larger eggs (i.e., 8 dams with EW $\geq$ 73.5 mg) than in the dam group with lower average EW. In addition, all the 10 abnormal eggs observed at hatching were bred by 5 dams from this dam group with larger eggs.

4. Discussion

4.1. *Evidence for variation in reproductive success in farmed trout*

Family variance in reproductive success was identified in our study from fertilization to three weeks after the first feeding. It was mainly due to the stage between fertilization and hatching (Seh) because no family differences in progeny survival were observed from hatching to three weeks after the first feeding (Shf) (Tables 3 and 4). Only dam contributions to the next generation were significantly unbalanced. No significant unbalanced contribution was observed for sires, probably because our mating plan was designed to avoid sperm competition (i.e., one-by-one male fecundation with an excess of sperm), which is known to induce variance in family size (Gage et al., 2004; Wedekind et al., 2007). One-by-one male fecundation of dam egg pools is a usual practice in trout breeding programs. Even though the differences in offspring survival between extreme sires were insignificant, they were 11% and 12% at eyed egg stage in the two replicates. Such differences might have been significant should we have used a higher number of sires and/or more offspring per sire. These results confirm previous studies on early progeny survival in rainbow trout, for which maternal effects are always

Table 8
Phenotypic correlations between size and reproduction traits of the 15 dams at 3 years of age. p-values figure between brackets.

	PW	SW	EN	RF	CF	EW	ED	Fdam
FL	0.689 * *	0.516 *	0.362	-0.13	-0.087	0.429	0.511 *	-0.263
PW		0.207	0.047	-0.55 *	-0.012	0.512 *	0.535 *	-0.385
SW			0.952 * **	0.64 * *	0.202	-0.022	0.135	-0.198
EN				0.79 * **	0.181	-0.322	- 0.139	-0.217
RF					0.14	-0.64 * *	- 0.49 *	0.03
CF						-0.023	- 0.132	0.094
EW							0.910 * **	0.053
ED								-0.118

FL: Female fork length; PW: Post-spawning weight; SW: Spawning weight; EN: egg number; RF: Relative fecundity; CF: Weight of coelomic fluid; EW: Average egg weight; ED: Egg diameter *** p-value < 0.001** p-value < 0.01* p-value < 0.1

Table 9
Pearson correlations between dam performances and progeny survival rates from eyed egg stage to 3 weeks after the first feeding.

	Se	Sh	Sf	Seh	Shf
FL	-0.07	-0.12	-0.03	-0.15	0.38
PW	-0.45 *	-0.54 *	-0.46 *	-0.49 *	0.36
SW	0.50 *	0.54 *	0.58 *	0.40	0.11
EN	0.50 *	0.61 *	0.66 * *	0.53 *	0.18
RF	0.62 * *	0.78 * **	0.78 * **	0.72 * **	-0.05
CF	0.21	0.20	0.11	0.12	-0.34
EW	-0.09	-0.31	-0.38	-0.50 *	-0.27
ED	-0.16	-0.24	-0.29	-0.27	-0.18

FL: Female fork length; PW: Post-spawning weight; SW: Spawning weight; EN: egg number; RF: relative fecundity; CF: Weight of coelomic fluid; EW: Average egg weight; ED: Egg diameter; Se: survival from fertilization to eyed egg stage; Sh: survival from fertilization to hatching; Sf: survival from fertilization to three weeks after first feeding; Seh: survival from eyed egg stage to hatching; Shf: survival from hatching to three weeks after first feeding.
* ** p-value < 0.001 * * p-value < 0.01 * p-value < 0.1

detected, but sire effects are low (Patton et al., 2007) or absent (Nagler et al., 2000). In the study by Patton et al. (2007), the sire effect may be at least partly confounded with a dominance effect because dams were mated with a single male. In chum salmon, significant sire and dam effects on early survival traits were identified by Smoker (1986). Similar results to ours were observed *in brown trout,* i.e., important maternal effects on offspring survival, but no sire effects when sperm competition was avoided (Régnier et al., 2010; Vandeputte et al., 2002).

As previously found by Rye et al. (1990), we did not observe significant phenotypic correlations between offspring survival at the different stages of larval development (Table 5, Fig. 5), because these various traits might be influenced by different determinants, pre-hatching survival being more strongly influenced by egg quality and maternal effects than post-hatching survival which is more linked to environmental conditions.

4.2. Importance of the genetic factors explaining early survival in a cohort of farmed trout fry

We did not observe any significant additive genetic variance on early survival traits. Estimated heritability for survival traits (at hatching or 3 weeks after first feeding) was low (respectively 0.20 and 0.13 under threshold models, but only 0.01 under linear models) in our study. Low to moderate heritability values (ranging from 0 to 0.29 taking into account the binary nature of survival traits) were also reported for early survival in different species of salmonids (*Oncorhynchus mykiss* and *Salmo salar*: Kanis et al., 1976; Gall and Gross, 1978; Rye et al., 1990; Houde et al., 2013, 2015; Vehviläinen et al., 2008; *Salvelinus fontinalis*: Robison and Luempert, 1984; *Arctic char*: Palaiokostas et al., 2020). However there was high uncertainty on most of these previous estimates and heritability may have been overestimated because maternal and/or dominance effects were not well accounted for in the models. Duenk et al. (2017) have demonstrated that including dominance effects was always equally or more accurate than the simple additive genetic model, even with a small sample size or in the absence of dominance.

In our study, heritability of survival did not significatively change between hatching and 3 weeks after the first feeding. The low mortality levels (4.1% for Seh and 7.2% for Sef) may limit the detection of genetic variation in early survival and may lead to low estimates of heritability in our study. The additive genetic coefficients of variation of early survival from eyed egg stage to hatching or to three weeks after first feeding, measuring their evolvability (Houle, 1992) were also very low, 0.74%, and 1.31%, respectively. This means that selection may not be efficient in improving survival from the eyed-egg stage to hatching or 3 weeks after first feeding. However, our experiment was based on a unique cohort with progeny bred from only 15 dams and 9 sires that were randomly sampled from a population with about 10 times more breeders. Uncertainty on our parameter estimates is a consequence of this small sampling set and further analysis on subsequent cohorts should confirmed our first estimates.

Under linear models (Table A.4), extremely high dominance deviation effects were estimated in our study. These results have to be taken with caution as phenotypic variances were low and only a small dataset was used to fit complex genetic models. However, the full AMD model including dominance deviation effects gave the better goodness-of-fit under linear model (minimum AIC value, Table A.4), while the threshold AMD model did not converged. Our high estimates of dominance deviation variance for early survival traits is consistent with the high non-additive genetic variances observed in Atlantic salmon (Houde et al., 2013, 2015) for survival from fertilization to hatching and from hatching to yolk sac resorption. High dominance variance is theoretically linked to inbreeding depression, that has been shown to play a significant role in female reproduction traits in a selected rainbow trout line, even if no genome-wide inbreeding effect was observed (Paul et al., 2021). Indeed, many studies showed inbreeding depression on fitness-related traits due to high levels of parental and own individual inbreeding (*Oncorhynchus mykiss:* Aulstad et al., 1972; Kincaid et al., 1976a; Gjerde et al., 1983; Naish et al., 2013; *Oreochromis niloticus:* Fessehaye et al., 2009; *Salvelinus alpinus:* Palaiokostas et al., 2021). In our study, we did not estimate any significant effect of dam or sire inbreeding levels on offspring survival neither at hatching nor at the end-point of the experiment. However, Su et al. (1996) revealed that dam inbreeding impacts egg quality and may reduce progeny survival in rainbow trout. Fessehaye et al. (2009) demonstrated that sire inbreeding could influence reproductive success in Nile tilapia, with an inbreeding depression effect observed for the number of progeny when males are in competition (which was not the case in our study).

In addition, we did not observe any significant difference in the numbers of dead fry among offspring with inbreeding levels over the average (Table A.6). On the contrary, Gjerde et al. (1983) and Aulstad et al. (1972) estimated inbreeding depression effects around 10% on survival from eyed egg stage to hatching in rainbow trout populations. Gjerde et al. (1983) also indicated inbreeding depression effects ranging from 5% to 11% on offspring survival from hatching to first feeding and

from the first feeding to 6 weeks after the first meal. However, these estimations were based on an experimental line with very high inbreeding levels (from 0.25 to 0.50) due to full-sib mating. Kincaid et al. (1976a) showed a high inbreeding depression effect on early survival in a rainbow trout population with high inbreeding levels (from 0.25 to 0.375). In our study, parents were weakly related, and there was no mating between full-sibs. Therefore, the inbreeding levels of the offspring remained moderate, with an average value of 0.10 and a maximum value of 0.25 (Table 1), which may explain why we did not observe any significant inbreeding depression effects compared to previous studies. Even though we did not observe a significant effect of genome-wide inbreeding on offspring survival, it does not mean that inbreeding depression is not occurring in some local regions in the genome, as Paul et al. (2021) revealed for female reproduction traits in rainbow trout.

Kincaid (1976b) showed no effect of inbreeding on the egg hatchability stage in a rainbow trout population but a higher inbreeding effect on fry survival in Kincaid (1976a). Houde et al. (2011) also observed no significant differences in offspring survival between inbred and non-inbred lines. In addition, Moss et al. (2007) highlighted that inbreeding has no effect on Pacific white shrimp survival in normal conditions, but a severe inbreeding depression on survival appears after exposure to viral pathogens. Their study proves that inbreeding may play a major role when life conditions change to extreme ones. In consequence, even if we did not identify any inbreeding depression effect on early survival in rainbow trout in our experimental conditions, we cannot exclude that inbreeding effects may reveal in less favourable rearing conditions.

4.3. Importance of maternal phenotypes on fry survival

Compared to our estimates based on animal models with maternal effects, higher proportion of phenotypic variances of egg, alevin or fry survival in salmonids species were explained by maternal effects under sire-dam models (Kanis et al., 1976; Rye et al., 1990; Houde et al., 2013, 2015). These previous results showed that heritability estimates derived from the dam components of variance were substantially higher (between 0.15 and 0.58 from eyed-egg stage to hatching and between 0.07 and 0.86 from hatching to first feeding) than those derived from the sire components, revealing that additive genetic effects were small, but non-additive genetic effects and/or maternal environment effects explained a high proportion of early survival in salmonids. However experimental designs and statistical models used in these previous studies did not allow to disentangle additive genetic, dominance deviation, maternal genetic and maternal environmental effects from the dam variance components.

In an attempt to understand which biological factors may underlie the maternal effects observed on early survival, we estimated Pearson correlations between various dam performances and offspring survival rates (Table 9). Because there is information on only 15 dams, most correlations are not statistically different from zero. This limits the interpretation of the results; however, some challenging results deserve discussion.

Whatever the stage, favourable correlations were estimated between offspring survival and fecundity traits (SW, EN, and RF). This is consistent with previous results on rainbow trout (Estay et al., 2021), showing a significant positive association between relative fecundity (RF) and progeny survival at the eyed egg stage. However, some weak negative trends between fecundity traits and survival stages (at the eyed egg, hatching, and swim up) were identified in another cultured stock rainbow trout (Kanyılmaz et al., 2016). In lake whitefish, survival until hatching and fecundity traits were not correlated (Wedekin and Müller, 2004).

In our study, as in many others in rainbow trout (Su et al., 1996; Gall and Neira, 2004; Solberg et al., 2014; Islam et al., 2021; Estay et al., 2021), results support the evidence that larger females produce larger eggs (higher EW average) than smaller females.

Our results, showing no significant association between egg size and survival contradict those of many studies (Bagenal, 1969; Wallace and Aasjord, 1984; Beacham and Murray, 1985; Rana, 1985; Marteinsdottir and Able, 1992) that showed that the survival of fry derived from larger eggs was significantly better, probably because these fries would be bigger. Here we even observed an almost significant negative correlation between egg weight and survival from eyed egg stage to hatching (Table 9, p-value = 0.06). An explanation for this excess in egg mortality may be the over-ripening of the larger eggs as all observed abnormal embryos at hatching came from the dams with the heaviest average egg weights. Indeed, some females may have reached maturity a few days before the others, inducing greater hydration and, therefore, larger eggs without their over-ripening being visible but potentially inducing developmental defects in the offspring (*Salmo salar*: Horreo et al., 2008; *Leuciscus idus*: Nowosad et al., 2018).

We observed that dams with heavier eggs had more malformed progenies. In the same way, Wallace and Aasjord (1984) observed that progeny groups with higher egg size in Arctic charr have higher fry mortality due to malformations. These observations deserve further attention by salmonid breeders as increasing egg size was initially thought to be an interesting way to increase alevin survival. Some studies demonstrate that the quantity and quality (such as lipid, protein composition, and triiodothyronine concentration) of egg reserves are crucial for fish offspring early survival (Brown et al., 1988; Greenblatt et al., 1989; Gisbert et al., 2000; Stuart et al., 2020). According to Stuart et al. (2020), the egg quality (lipid and protein) is increased with egg size because of a higher metabolic reserve (Brooks et al., 1997). Besides, Berg et al. (2001) and Régnier et al. (2013) demonstrated that small eggs are not always those of lesser quality because small eggs allow, for example, to have a better protein content than larger eggs. Even if a larger egg produces a larger fry, this advantage can be masked by other environmental determinants of growth (Bromage et al., 1992), and egg size does not appear to be an essential indicator of egg quality in farmed rainbow trout populations (Brooks et al., 1997). In addition, Einum and Fleming (1999) observed that differences in offspring's survival from small and large eggs decreased with increasing environmental quality. So, in high-quality environments (facilities, farmed environments), no egg size effect should be observed on offspring's survival. To finish, egg size was uncorrelated with progeny survival in various studies and fish species (*Oncorhynchus mykiss*: Springate and Bromage, 1985; Herbinger et al., 1995; Blanc, 2007; *Salmo trutta fario L.*: Vandeputte et al., 2002; *Cyprinius carpo L.*: Vandeputte et al., 2004; *Salvelinus alpinus*: Jónsson, Svavarsson, 2000; Leblanc et al., 2016).

5. Conclusion

This study highlights the biological factors underlying early survival and identifies maternal disequilibrium contributions to the next generation in a domesticated rainbow trout line. There is no evidence for inbreeding depression on offspring survival in the range of inbreeding values and environmental conditions of this study. Heritability of early survival is low, not statistically different from zero, but maternal effects explain a larger amount of the phenotypic variance of embryo survival. While egg size has no significant effects on early survival, dam weight and fecundity seem to play important roles underlying the maternal effects observed on embryo and fry survival. Further studies are needed to well understand these roles and to confirm the existence of non-additive genetic factors impacting early survival in rainbow trout.

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CRediT authorship contribution statement

Katy Paul: Investigations, Methodology, Software, Formal analysis, Writing – original draft. **Pablo Pelissier, Lionel Goardon, Nicolas Dechamp, Jeanne Danon, Lydia Jaffrelo, Charles Poncet**: Investigation, Resources. **Mathilde Dupont-Nivet**: Conceptualization, Draft reviewing. **Florence Phocas**: Supervision, Conceptualization, Methodology, Investigation, Resources, Formal analysis, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2023.101523.

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