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Food Quality and Life-History Genotype Influence Maturation and Reproductive Traits in Female Atlantic Salmon

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ABSTRACT

Age at maturity is an important life-history trait, often showing sex-specific variation, contributing to life-history diversity in many species. Atlantic salmon (*Salmo salar*) are an excellent model system to investigate genetic and environmental factors affecting sex-specific maturation, yet few laboratory studies have focused on females as they mature later than males, on average. Using a 4-year common-garden experiment of Atlantic salmon, we assessed the influence of diet (low-fat vs. control) and *vgl3* (a candidate gene influencing maturation age) on maturation and related phenotypic traits of female Atlantic salmon derived from two second-generation hatchery populations. We found the early-maturation associated E allele to be additively associated with a higher probability of maturation. Heritability of maturation was estimated to be 0.295, with *vgl3*'s contribution to phenotypic variance being ~2%. In addition, body condition measured in the spring prior to spawning influenced maturation. Body condition, in turn, was influenced by population and diet. The more northern Oulu population and the low-fat diet were associated with lower body condition compared to the more southern Neva population and the control diet. Moreover, there was an interaction between population and diet on body condition, suggesting that populations may respond differently to nutrient availability. These results broaden our understanding of the processes underlying sex- and population-specific maturation and demonstrate that genes and environment influence age at maturity in a species that displays sex-specific variation in maturation.

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1 | Introduction

Understanding the processes governing life-history trait variation is at the forefront of evolutionary biology research (Stearns 2000). The rapid development of genomic tools over the past two decades has allowed us to gain a fine-scale understanding of the genetic basis of life-history traits in various taxa at both single-gene and genomic-region levels in a broad range of animals. For example, specific genomic regions are known to explain variation in reproductive strategies in ruffs (Küpper et al. 2016; Lamichhaney et al. 2016; Loveland et al. 2025), developmental time in *Tribolium* beetles (Cheng et al. 2024), coloration and life-history strategies in *Colias* butterflies (Woronik et al. 2019) and migration timing and age at maturity in several salmonid fishes (Ayllon et al. 2015; Barson et al. 2015; Hess et al. 2016; Prince et al. 2017). These studies have expanded our knowledge of the genetic basis of life-history traits and offer an opportunity for follow-up studies that look beyond the genetic associations and into how the genomic regions or candidate genes mediate traits independently or via interactions with environmental factors.

Atlantic salmon, *Salmo salar*, is one of the species for which we have gained a deeper understanding of the genetic basis of life-history trait variation in recent years, especially with respect to age at maturity (Ayllon et al. 2015; Barson et al. 2015; Sinclair-Waters et al. 2020). Atlantic salmon have a complex life cycle often spanning both freshwater and marine environments (Jonsson and Jonsson 2011; Thorstad et al. 2010). Consequently, they exhibit great variation in different life-history traits, such as time spent in freshwater or at sea, age or size at maturity, and number of reproductive events (de Eyto et al. 2015; Erkinaro et al. 2019; Mobley et al. 2020; Persson et al. 2023). Age at maturity is a key life-history trait tightly linked with fitness that is affected by both environment and genetics in salmon (Mobley et al. 2021). Maturation in salmon has both a strong single-gene (Ayllon et al. 2015; Barson et al. 2015) and polygenic component (Sinclair-Waters et al. 2020). Allelic variation in the candidate gene *vgll3* explains close to 40% of variation in sea age at maturity in European Atlantic salmon populations (Barson et al. 2015). In relation to age at maturity, *vgll3* has two alleles, the E and the L allele, associated with early and late maturation, respectively (Barson et al. 2015).

In many species, males and females reach sexual maturity at different ages (Fairbairn 2013; Roff 2002; Stamps and Krishnan 1997). In salmonids, age at maturity often shows sex-specific variation, where, on average, females mature at an older age and larger body size compared to males (Erkinaro et al. 2019; Evans et al. 2019; Fleming and Einum 2011; Mobley et al. 2020, 2024; Tréhin et al. 2021). Furthermore, patterns of sex-specific dominance for age at maturity at the *vgll3* locus have been reported in some wild populations, with the heterozygous EL males maturing at a younger age compared to heterozygous females (Barson et al. 2015; Besnier et al. 2024; Czorlich et al. 2018; Miettinen et al. 2024; Mobley et al. 2024; Raunsgard et al. 2023). Older female age at reproduction is associated with higher reproductive fitness in many taxa (Kopf et al. 2024). Similarly, for female salmon, body size is an important determinant of reproductive fitness, as larger body size not only allows for higher fecundity, but may also be associated with a

better ability to dig and defend nests at the spawning grounds (Fleming 1996; Heinimaa and Heinimaa 2004). Thus, older age at maturity offers a fitness benefit, but simultaneously there is a trade-off, as a longer time spent in the marine environment is associated with a higher risk of mortality (Mobley et al. 2021).

Reproduction and age at maturity are tightly linked with individual growth, developmental rate, and environmental conditions in a range of species (Bernardo 1993). In Atlantic salmon, environmental factors such as temperature and diet can influence growth and available energy reserves and, consequently, age at maturity (Jonsson and Jonsson 2011; Mobley et al. 2021; Taranger et al. 2010). Maturation is an energy-demanding process where organisms divert energy previously allocated to somatic growth into reproduction (Ginther et al. 2024) and larger energy reserves may be associated with a higher probability of maturation (Bernardo 1993; Rowe et al. 1991; Shearer and Swanson 2000; Taranger et al. 2010). Salmon allocate almost 60% of their energy stores to reproduction, and in female salmon, a major part of that energy is allocated to egg production (Fleming and Einum 2011). Salmon are generalist feeders, and at sea, they feed on energy-rich prey such as herring (*Clupea harengus*), capelin (*Mallotus villosus*), and sprat (*Sprattus sprattus*) (Hansson et al. 2001; Haugland et al. 2006; Rikardsen and Dempson 2011; Salminen et al. 2001). If the availability of prey species is altered, for example, because of changes in the composition of marine food webs, salmon feeding opportunities may be reduced both in terms of the overall quantity of prey as well as the availability of energy-rich prey species (Czorlich et al. 2022; Litzow et al. 2006; Vollset et al. 2022). Therefore, the ability of individuals to acquire energy for maturation, be it through the quantity or energetic quality of their feed, can influence growth and consequently size and age at maturity (Jonsson et al. 2012, 2013; Vollset et al. 2022).

Since the discovery of the association between *vgll3* and age at maturity, a number of studies have investigated how *vgll3* relates to different life-history traits in Atlantic salmon with a view to understand the mechanisms behind the gene's association with maturation. The association between *vgll3* and sea age at maturity has been demonstrated in wild populations for both males and females (Czorlich et al. 2018; Miettinen et al. 2024; Mobley et al. 2024; Raunsgard et al. 2023), and replicated for males in common-garden experiments in hatchery populations (Åsheim et al. 2023; Debes et al. 2021) and in an aquaculture strain (Ayllon et al. 2019; Sinclair-Waters et al. 2022). In addition to age at maturity, *vgll3* has been associated with behavioural traits (Bangura et al. 2022, 2024), body condition (Debes et al. 2021; House et al. 2023), seasonal lipid phenotypes (House et al. 2025), migration activity (Niemelä et al. 2022) and aerobic scope (Prokkola et al. 2022). Though the link between *vgll3* and age at maturity has been studied in females in wild populations (Barson et al. 2015; Czorlich et al. 2018; Miettinen et al. 2024; Mobley et al. 2024; Raunsgard et al. 2023), only one previous study has investigated *vgll3*'s role in female maturation in a controlled common-garden experiment (Ayllon et al. 2019). In that study, no association between *vgll3* genotype and maturation age in the Mowi aquaculture strain was found (Ayllon et al. 2019). Therefore, there is an incomplete understanding of how *vgll3* and the environment influence age at maturity in female Atlantic salmon.

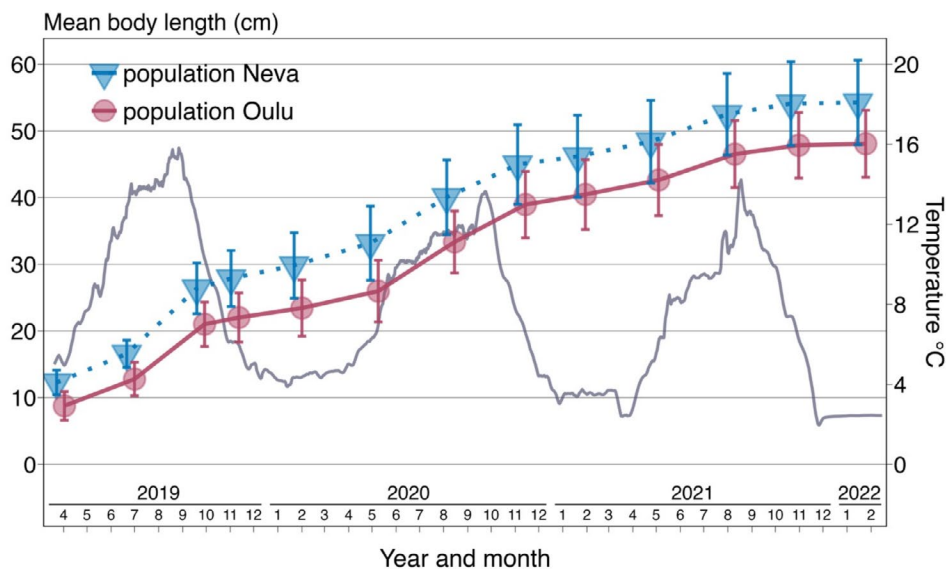


FIGURE 1 | Growth of female Atlantic salmon represented as mean body length in centimetres during the common-garden experiment. Length was measured roughly every 3 months following PIT tagging in April 2019 until the termination of the experiment in February 2022. Body length is plotted separately for the Oulu and Neva populations, with feed treatments pooled together. Error bars indicate one standard deviation. The grey line represents the seasonal water temperature fluctuation (7-day rolling average) in the experimental tanks. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/nve.17735)]

In this study, we conducted a common-garden experiment to investigate how the environment, namely energy content of the diet, and variation in *vgll3* influence maturation and reproductive traits in 4-year-old female Atlantic salmon. With this experiment, we aimed to answer the following questions: (1) Does *vgll3* influence age at maturity in female Atlantic salmon, and is the potential influence similar to that reported in wild populations? (2) does diet energy content influence maturation? (3) are there population-specific differences in maturation response to diet or in how *vgll3* genotype influences maturation? In addition to maturation, we investigate the effect of diet, population and *vgll3* on reproductive traits, such as body condition, body size and fecundity to assess how these traits are affected by energy resources and genetics. We also estimate heritability of maturation and the contribution of *vgll3* to phenotypic variance to better understand the potential for selection to shape age at maturity.

2 | Methods

2.1 | Populations and Cross-Design

Detailed descriptions of the Atlantic salmon hatchery populations used in this study, the crossing design and rearing conditions are provided in Åsheim et al. (2023) and the description of the egg incubation phase in Debes et al. (2020, 2021). As we were interested in studying population-specific maturation responses to environmental factors and the influence of *vgll3* on maturation, the Atlantic salmon used in this study represent two genetically distinct Atlantic salmon populations from the Baltic Sea: the Neva and the Oulu populations, named after their locations of origin (Säisä et al. 2005). Broodstocks originating from these populations are maintained by the Natural Resources Institute Finland (Luke) for compensatory stocking purposes in Finnish rivers with hydropower regulation. The

southern Neva population is routinely stocked into the River Kymijoki (60.48°N, 26.89°E), which drains into the Gulf of Finland, whereas the northern Oulu population is stocked into the river Oulujoki (65.01°N, 25.27°E) draining into the Bothnian Bay. The broodstocks maintained at the Luke hatcheries are renewed every few years with new broodstocks created from mature adults caught during their spawning migrations in their respective rivers. The parental salmon of our experimental cohorts were from first-generation hatchery broodstocks whose parents had successfully completed a marine migration. The large number of mature individuals with known genetic backgrounds in the Oulu and Neva broodstocks allowed us to cross individuals based on their *vgll3* genotype and create a large number of families with each *vgll3* genotype while controlling for family structure.

To create our experimental cohorts, male and female salmon with homozygous *vgll3* genotypes (EE and LL) were crossed in multiple 2 × 2 factorials (13 and 17 factorials for the Oulu and Neva populations, respectively) with each factorial resulting in four families where all offspring within a family had the same *vgll3* genotype (EE, EL/LE or LL). In this study, the heterozygotes are treated as one genotype, EL.

The eggs were fertilised in October 2017 at the Viikki campus of the University of Helsinki (60.23°N, 25.02°E) and moved to the common-garden experimental facilities at Lammi Biological Station (LBS; 61.05°N, 25.04°E, Lammi, Finland) at the first-feeding stage in February–March 2018. Alevins were allocated to six circular tanks (Ø277 cm, maximum water volume 4.6 m³), with evenly mixed populations, *vgll3* genotypes and families in each tank. Continuous water flow into the tanks was created by pumping water (UV-sterilised and heated by ~1°C prior to entering the tanks) from the nearby lake Pääjärvi, with the water temperature in the experimental tanks following the lake's natural temperature

fluctuations (Figure 1). The average water temperature in the tanks during the year prior to spawning was $6.82^{\circ}\text{C} \pm 3.17^{\circ}\text{C}$ (min 2.14°C , max 18.10°C) and across the whole experiment $7.68^{\circ}\text{C} \pm 3.93^{\circ}\text{C}$ (min 0.22°C , max 18.69°C). In March 2021, heating of the incoming water was terminated, and individuals were redistributed into 12 tanks in order to reduce biomass. Light conditions in the experimental tanks followed the local photoperiod (Figure S1). Water salinity was not modified during the experiment, and the salmon were only reared in freshwater conditions.

2.2 | Tagging, Phenotypic Measurements, and Genetic Analyses

In April 2019, all salmon were tagged with 12 mm passive integrated transponder (PIT) tags enabling identification of individuals and thus tracking of individual size and growth from that point onwards. Fin clips were taken for genetic parentage assignment, and thereby population and *vgll3* genotype of the individuals using a 177 single nucleotide polymorphism (SNP) panel (Aykanat et al. 2016) sequenced on an Illumina platform (MiSeq or Next-Seq) as described in Debes et al. (2021).

All fish were measured four times per year with approximately 3-month intervals between each measurement. Prior to handling, the salmon were anaesthetised with sodium bicarbonate-buffered tricaine methanesulphonate (MS-222; concentration 0.125 g l^{-1}). During the measurements, wet body mass (in g) and fork length (in mm) of the individuals were recorded. These body size measurements were then used to calculate Fulton's condition factor (*K*) as a measure of body condition with the formula $K = 100 \times (\text{mass (g)}/\text{fork length}^3 (\text{cm}))$ (Heincke 1908). In addition, migration phenotype (smolt versus parr) was recorded using the presence of parr marks. Individuals were considered smolts after the last record of visible parr marks. By August 2020, all female salmon included in this study had smoltified.

There were 1142 female salmon with known genetic backgrounds (*vgll3* genotype, family, population) which were monitored throughout the experiment from PIT tagging in April 2019. By November 2021, a total of 110 individuals had died (mortality of $\sim 9.6\%$), 219 individuals were sampled for use in other studies (only Neva individuals, balanced in regards to *vgll3* genotype, family and feed treatment), and 59 were culled to reduce biomass in the tanks (balanced across *vgll3*, population, family and feed treatment). These sampled and culled individuals were not included in the mortality estimate.

2.3 | Feed Treatment

In July 2019, 1 year and 4 months after exogenous feeding had commenced, a feed treatment was started, whereby the salmon were fed either a control or a low-fat feed. The control feed was standard commercial fish feed (Hercules Baltic blend; Raisioaqua, Raisio, Finland), whereas the low-fat feed was the same standard feed but manufactured with a lower fat content. This lower fat content resulted in $\sim 22\%$ lower energy content

(kJ/100 g) for the low-fat feed (feed content analyses for each feed batch were conducted by Synlab Oy, Karkkila, Finland). Feed was administered *ad libitum* to the tanks of both treatments using automatic feeders (Arvo-Tec Oy, Huutokoski, Finland) during daylight hours, and the feed pellets were size-matched with the body size distribution of fish in each tank. The nutritional contents of the different pellet sizes and their use dates are presented in Tables S1 and S2. By the spawning season of autumn 2021, the fish had been fed on one of the two diets for approximately 2 years and 4 months.

2.4 | Maturation

Maturation status of the females ($n = 753$) was assessed in November 2021 when the salmon were 4 years old. During the previous 2020 spawning season, there were 59 mature females in our experimental cohorts (Table S3 and Maamela et al. 2023). The previously mature individuals that were still alive in November 2021 ($n = 21$) were removed from the analyses presented here due to their low number and the complications the inclusion of repeat spawning and previously mature individuals would have introduced in the analyses. Thus, none of the females included in this study had matured previously, and this study is only assessing first-time maturation in the 2021 spawning season.

During the spawning of 2021, there were females from 46 families of the Oulu population and 39 families of the Neva population from 13 and 14 2×2 factorials, respectively. Maturation was assessed between 1st–18th November 2021 and between 31st January–8th February 2022 based on external characters as in Maamela et al. (2023). Briefly, females with an extended cloaca and releasing eggs when gentle pressure was applied to the abdomen were considered mature, and females with an absence of these signs were considered immature. The majority of the mature females were releasing eggs in November. The February time point was used to confirm that the females that were maturing in November, but that were not yet releasing eggs, indeed matured later during the spawning season. Fecundity (egg number) was measured in a subsample of 318 females in November 2021. The subsampled individuals were randomly chosen from the mature females with the aim of having all *vgll3* genotypes represented as equally as possible within feed treatments for both populations. Since our experiment included more fish from the Oulu population ($n = 469$) compared with the Neva population ($n = 284$), the study has a higher representation of Oulu individuals for the fecundity analysis. In total, we analysed fecundity for 248 and 74 females from the Oulu and Neva populations, respectively. The number of sampled females per *vgll3* genotype, feed treatment and population is summarised in Table S4.

The females were hand stripped by gently massaging the abdomen to extract the eggs. The total wet mass (g) of the egg clutch was obtained by weighing after straining off the ovarian fluid with a metal sieve (mesh size 2 mm). Three replicates of 10 eggs each were weighed (to 0.0001 g accuracy) to obtain individual egg wet weight. Fecundity of the individuals was calculated by dividing the total egg clutch mass by the mean individual egg wet weight.

2.5 | Statistical Methods

2.5.1 | Samples Used in the Models

A total of 730 female salmon, which were spawning for the first time and for which phenotypic, genotypic and population information was available, were included in the final models for maturation probability, body size and body condition. An overview of the number of female salmon in the different treatments is summarised together with the observed maturation rates in Table S5.

2.5.2 | Common Model Structures

We analysed the effect of diet, *vgll3* and population on maturation, body condition, body length and fecundity with generalised and general linear mixed effect models. The common covariates used in all models were feed treatment (control, low-fat) and population (Neva, Oulu), both coded as two-level factor variables. To test for additive effects of *vgll3* genotypes, the genotypes were coded as -1, 0 and 1 for the LL, EL and EE genotypes, respectively. Though dominance effects at the *vgll3* locus on age at maturity have been documented previously in the wild (Barson et al. 2015; Czorlich et al. 2018; Mobley et al. 2024), none have been detected in controlled conditions for males (Åsheim et al. 2023; Debes et al. 2021). Similarly, for female salmon, the previously found dominance effects have been weaker or population- or age-specific compared to males (Barson et al. 2015; Czorlich et al. 2018) and in line with this, other studies have shown the effect of *vgll3* to be completely additive in females (Miettinen et al. 2024; Raunsgard et al. 2023). Therefore, we excluded dominance effects in our models in order to reduce model complexity and aid model fitting. Body length and body condition were mean-centred and standard deviation-scaled before being included in the models. We used body size and body condition measurements taken in May 2021, approximately 5 months prior to spawning, in all analyses. This spring timepoint was chosen for the measurements as we wanted to model the effect of available energy for reproduction before the individuals had allocated energy towards gonad development for the coming spawning season (Åsheim et al. 2023; Debes et al. 2021).

2.5.3 | Maturation Model

Maturation probability was analysed using a generalised linear mixed effect model (GLMM) with maturation coded as a Bernoulli-distributed binary variable (0 for immature, 1 for mature) with a logit-link function. The *vgll3* genotype, population, feed treatment, body length and body condition were included as fixed effects in the model. In addition, we included two-way interactions between *vgll3* genotype, population and feed treatment to assess genotype-by-environment (GxE) effects on maturation probability. An interaction between *vgll3* and body condition was also included as previous studies have found *vgll3* to be associated with the body condition of Atlantic salmon (Debes et al. 2021; House et al. 2023). Initially, we also included a three-way interaction between *vgll3*, population and feed, as the observed maturation rates indicated that such an interaction might be present (see Figure 2). There was no clear three-way interaction effect on maturation (the 95% credible interval overlapped with zero) and we removed this interactive effect from the final model in order to aid model fitting.

Family structure and relatedness among individuals were accounted for using the animal model approach (Wilson et al. 2010) by including the effect of an individual animal in the model as a random effect. This effect of an individual was fitted using the additive genetic relatedness matrix obtained from the pedigree. Our pedigree included family relationships up to the grandparental level. These grandparental individuals were the Atlantic salmon that successfully completed a sea migration and were the founders of the broodstock created by LUKE (see information about broodstocks above and in Åsheim et al. 2023). By utilising the pedigree-based relatedness matrix to correlate the additive genetic random effects in the model, we were able to obtain estimates of additive genetic variance (V_A) that were then used to calculate the heritability of maturation. Heritability (h^2) was calculated by dividing the sum of V_A and the additive variance contributed by *vgll3* ($V_{A,vgll3}$) by the total phenotypic variance estimate (V_P) calculated as the sum of the different variance components ($V_P = V_A + V_{A,vgll3} + V_{\text{tank}} + V_{\text{residual}}$). $V_{A,vgll3}$ was estimated as in Debes et al. (2021) and in Åsheim et al. (2023) using the formula $V_{A,vgll3} = 2pq(\alpha_{vgll3})^2$, where p and q are the *vgll3* allele frequencies in the data and α_{vgll3} is the weighted average of the

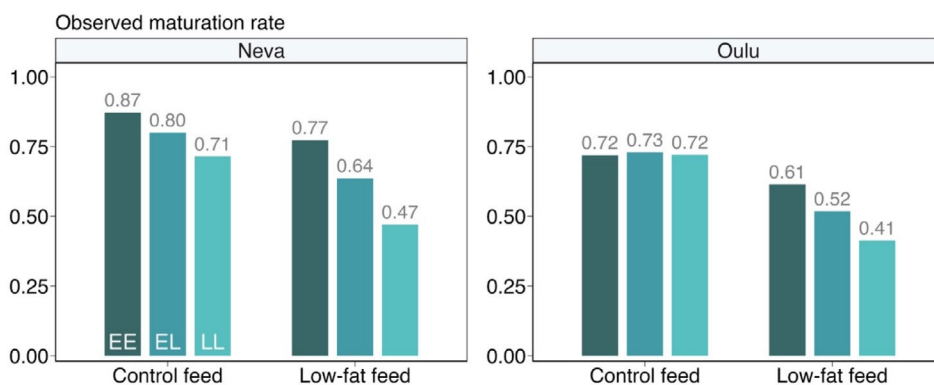


FIGURE 2 | Observed proportions of *vgll3* genotype-specific maturation in female Atlantic salmon from two populations (Neva, Oulu) in two feed treatments. The colours indicate the three different *vgll3* genotypes (dark blue = EE, blue = EL, light teal = LL). The exact maturation rates and number of salmon per group are presented in Table S5. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

vgll3 model regression coefficient estimates within treatment groups (i.e., populations and feed treatments). V_{tank} was obtained from the model's random tank effects. Due to the difficulty in estimating V_{residual} in a GLMM threshold model with a logit-link function, we follow Nakagawa and Schielzeth (2010) and de Villemereuil (2023) in setting V_{residual} to $\pi^2/3$ for the heritability calculations. $V_{A,vgll3}$ was also used to calculate SNP heritability (*vgll3*'s contribution to total phenotypic variance) by dividing $V_{A,vgll3}$ by V_p .

Raw parameter estimates from the maturation model were converted from log odds ratios to odds ratios ($e^{\log \text{odds ratio}}$) in the text, thus giving the relative estimate of change in the odds of maturing. Odds are the probability of maturing divided by the probability of not maturing, and range from zero to infinity, which is simpler to model compared to probability, which is bound between zero and one.

2.5.4 | Body Condition, Length and Fecundity Models

We used linear mixed effect models with an identity-link function to investigate the effects of the focal traits and treatments (*vgll3*, population, feed treatment) on body condition, body length and fecundity. Similar to the maturation probability model, we added two-way interactions between all fixed effects.

In the fecundity model, we included body length and body condition of the individuals for which we had fecundity data as additional covariates as these traits are known to influence egg number in fish (Barneche et al. 2018). Based on the results of the body condition and length models (see Section 3), we also included two-way interactions between population and body length as well as population and body condition. An interaction between *vgll3* and body condition was also added. Fecundity was mean-centred and standard deviation-scaled before being included in the model to aid model fitting. In the plotted results, predicted fecundities have been back-transformed to the original scale.

2.5.5 | Modelling Technicalities and Assessment of Model Fits

All models were fit using Bayesian statistical methods. The models used four Hamiltonian Monte Carlo chains, each run for 3000 iterations, with the first 500 iterations discarded as warm-up. Thus, the models resulted in 10,000 realisations of the posterior distribution for each response variable. For all models (maturation, fecundity, body condition and body length), we set all priors for the intercept, parameter estimates and random factors as fairly noninformative normal distributions with a mean of zero and a standard deviation of one. These priors assume a 50% probability of maturation at the intercept and that there is no effect of any of the variables included in the model.

Models were assessed for convergence and autocorrelation based on a visual inspection of the trace and autocorrelation plots and by using R-hat values. All R-hat values were below 1.05, and the plots showed proper mixing of the chains. No autocorrelation was detected. In addition, model fits were checked

by calculating pareto k diagnostics and performing a visual posterior predictive check. The pareto k diagnostics found no highly influential points for the maturation, body condition or body length models, but two influential points (0.7%, $k > 0.7$) were found in the fecundity model.

2.5.6 | R Packages Used

All data analyses were done using Rstudio version 2023.12.1 running R v4.4.0 (R Core Team 2024). Data management and visualisation was done using the *tidyverse* package v2.0.0 (Wickham et al. 2019). The *loo* package v2.7.0 (Vehtari et al. 2017, 2024; Yao et al. 2018) was used to calculate pareto k model diagnostics. All Bayesian models were run using *rstan* v2.19.3 (Stan Development Team 2020) via the *brms* package v2.17.0 (Bürkner 2017, 2018, 2021).

2.6 | Ethics Statement

The experiments were approved by the Project Authorisation Board (ELLA) on behalf of the Regional Administrative Agency for Southern Finland (ESAVI) under experimental licence ESAVI/2778/2018.

3 | Results

3.1 | Overall Maturation Rates

Overall, 66.8% of the 730 female salmon in our experiment were mature, with population-specific maturation rates being 74.6% for Neva and 62.3% for Oulu individuals, respectively (Figure 2). Across populations, the observed *vgll3* genotype-specific maturation rates were 72.9%, 65.3% and 59.3% for the *vgll3* EE, EL and LL genotypes, respectively. Maturation rates were lower in the low-fat feed treatment (59.0%) compared to 75.7% in the control feed treatment. The highest maturation rate (87.2%) was observed for the *vgll3**EE individuals of the Neva population that were fed on the control diet. This was more than double the lowest maturation rate of 41.3% for *vgll3**LL Oulu individuals from the low-fat feed treatment (Figure 2, Table S5).

3.2 | Statistical Results for Maturation, Body Length and Body Condition Models

3.2.1 | *vgll3* Genotype Effects

Vgll3 genotype influenced maturation probability of female salmon (Figure S2, Figures 2 and 3, Table S8). The effect of *vgll3* was additive, with each added E allele increasing the relative odds of maturation by 2.41-fold ([95% CI: 1.07, 5.42], for Neva individuals in the control-feed group, of average body condition). We did not detect clear interactions between *vgll3* and feed or between *vgll3* and body condition on the probability of maturation (Figure 3). There was, however, an uncertain interaction (the 95% CI overlapped with zero, with 97.1% of the total posterior distribution being below zero and 2.9% above zero) between *vgll3* and population, whereby the additive effect of *vgll3* on

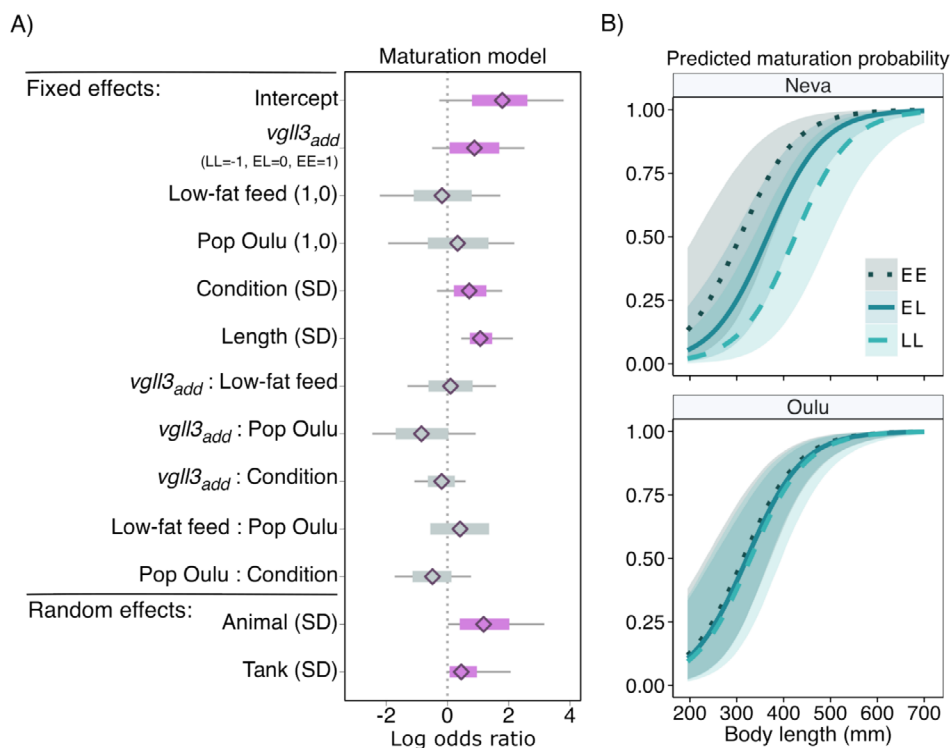


FIGURE 3 | (A) Parameter estimates (log odds ratio) and 95% credible intervals (CI) for the fixed and random effects obtained from the maturation model. The diamonds indicate the mean parameter estimates calculated from the posterior samples, the thick bars indicate the 95% CIs, and the thin bars the 100% CI. The thick bars are coloured purple if the 95% CI does not overlap zero. The scales of the fixed and random effect model parameters are indicated in the parentheses after the variable name. For categorical variables, the levels are 0 = Neva and 1 = Oulu for population, and 0 = control and 1 = low-fat for feed. Continuous variables were centred and standard deviation- (SD) scaled which leads to model estimates indicating the effect of increasing or decreasing the variable by one SD. Model intercept was set to 0 for all variables. Random effects standard deviations indicate the magnitude of variation among tanks and breeding values. Full model results are presented in Table S8. (B) Predicted maturation rates for female Atlantic salmon with different *vgl3* genotypes (dotted dark blue = EE; solid blue = EL; dashed teal = LL) from two different populations (Neva; Oulu) along body length (mm). Predictions were estimated using the maturation model with feed treatment set as the low-fat feed and body condition as the mean of all the female salmon included in the analysis. The shaded areas along the prediction lines represent the 95% CI. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

maturation was lower for the Oulu individuals and their predicted maturation probability lacked any *vgl3* effect (Figure 3). This interaction was likely driven by the Oulu individuals in the control feed treatment, where the effect of *vgl3* genotype on maturation was not evident (Figures 2 and 3).

Vgl3 genotype did not influence body length or body condition in the spring prior to spawning (Figures S4 and S5, Tables S9 and S10).

3.2.2 | Feed

Diet did not have a direct effect, meaning an effect which is independent of the effect of body condition, on maturation probability for females. The model estimate for the effect of feed on maturation was close to zero with a 95% credible interval that included zero (Figure 3). Diet did affect body condition, with the low-fat diet being associated with lower body condition (model estimate: -0.88 [95% CI: $-1.20, -0.54$]; Figure S4). There was an interaction between feed treatment and population on body condition whereby the decrease in body condition due to the low-fat diet was slightly larger in Oulu than in Neva individuals (model estimate: -0.22 [95% CI: $-0.44, -0.01$]; Figure 4). No effect of

feed was found on either body length (Figure S5) or fecundity (Figure 4).

3.2.3 | Population

We did not find a direct effect of population on maturation probability (Figure 3), but population influenced both body length (model estimate: -1.00 [95% CI: $-1.35, -0.65$]; Figure 1, Table S10) and body condition (model estimate: -0.56 [95% CI: $-0.87, -0.25$], Figure S4, Table S9). Oulu individuals were, on average, smaller (Figure 1) and had lower body condition (Figure S8) than the Neva individuals. For example, in May 2021, the mean body length of Oulu individuals was 42.6 ± 0.25 cm compared to 48.4 ± 0.38 cm for Neva (Table S6).

3.2.4 | Effects of Body Size and Body Condition on Maturation

Both larger body size and higher body condition in the spring prior to spawning were associated with a higher probability of maturation (Figure 3 and Figure S3). Body length had a slightly larger influence on maturation compared to body

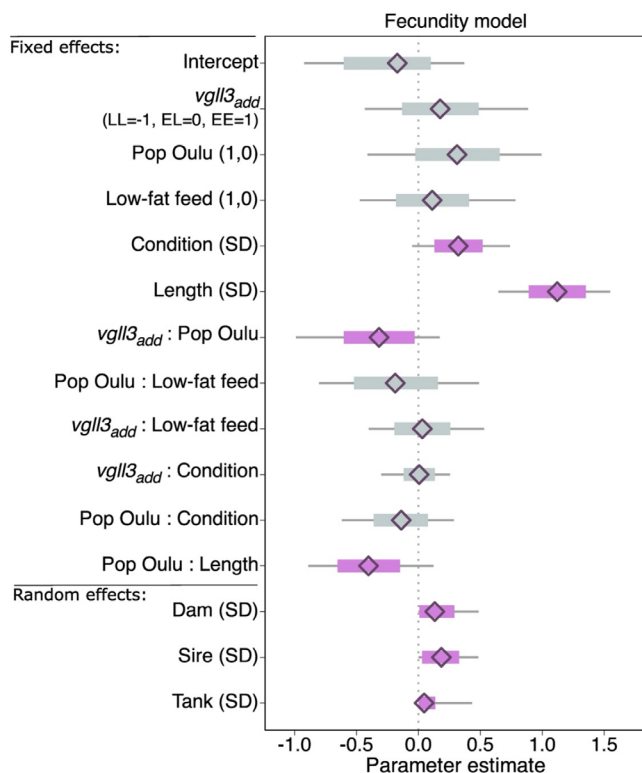


FIGURE 4 | Parameter estimates and 95% credible intervals for the fixed and random effects obtained from the fecundity model. The scales of the fixed and random effect model parameters are indicated in the parentheses after the variable name. For categorical variables, the levels are 0=Neva and 1=Oulu for population, and 0=control and 1=low-fat for feed. Continuous variables were centred and standard deviation- (SD) scaled which leads to model estimates indicating the effect of increasing or decreasing the variable by one SD. Model intercept was set to 0 for all variables. Random effects standard deviations indicate the magnitude of variation between tanks and between parents. The diamonds indicate the mean parameter estimates calculated from the posterior samples, the thick bars indicate the 95% CIs, and the thin bars the 100% CI. The thick bars are coloured purple if the 95% CI does not overlap zero. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

condition. An increase of one standard deviation in body length increased the odds of maturation by 2.92-fold [95% CI: 2.08, 4.30], whereas the effect of one standard deviation in body condition increased maturation odds by 2.04-fold [95% CI: 1.23, 3.55].

3.2.5 | Heritability

Heritability (h^2) of female maturation at 4 years old was 0.295 [95% CI: 0.064, 0.543]. We estimated the contribution of *vgl3* to phenotypic variance to be 0.02 [95% CI: 0.00, 0.065].

3.3 | Fecundity

Fecundity ranged from 728 to 6937 eggs, with the average being 2910 (Figure 5, Table S7). As expected, body size affected fecundity, with longer body length resulting in a higher egg number (model estimate: 1.12 [95% CI: 0.9, 1.35], Figures 4

and 5, Table S11). Population had an influence on the number of eggs a salmon produced; the mean fecundity of a Neva individual was 3750, whereas the mean fecundity was 2670 for an Oulu individual (Table S7). Interestingly, the fecundity-increasing effect of body length was not as strong for the Oulu individuals compared to the Neva, as indicated by the interaction term between population and length (model estimate: -0.40 [95% CI: $-0.65, -0.15$], Figure 4, Table S11). In addition, there was an interaction between population and *vgl3* genotype, where the additive effect of *vgl3* on fecundity was not as strong for the Oulu compared to Neva individuals (model estimate: -0.32 [95% CI: $-0.61, -0.04$], Figure 4 and Figure S6, Table S11).

4 | Discussion

We used Atlantic salmon as a model system to investigate the influence of a large-effect locus, population and environment on important life-history traits and most notably, on age at maturity. Despite the phenotypic optima for age and size at maturity differing between the sexes (Mobley et al. 2021), female Atlantic salmon have seldom been included in common-garden experiments studying maturation. This exclusion has left a gap in our knowledge of the genetic and environmental factors influencing age at maturity. In this study, we reared female salmon from two populations until 4 years old in a common-garden experimental setting where we manipulated the energy content of their diets and assessed the probability of maturing for the first time at this age. We found genetic effects on maturation and reproductive traits both at a single-locus level and at a population-of-origin level. *Vgl3* genotype influenced maturation probability, whereas population had an indirect effect on maturation via body condition, and an effect on fecundity. Additionally, a higher energy content diet was associated with higher body condition. As higher body condition was also associated with a higher probability of maturation, diet had an indirect effect on maturation via the available energy resources that could be allocated to reproduction. Thus, this study broadens our understanding of the factors influencing and processes underlying sex- and population-specific maturation.

4.1 | *Vgl3* and Female Maturation

We demonstrate that the *vgl3* locus influences female Atlantic salmon maturation in a controlled experimental setting similarly to how it affects female maturation in the wild (e.g., Barson et al. 2015; Besnier et al. 2024; Czorlich et al. 2018; Miettinen et al. 2024; Raunsgard et al. 2023). The effect of *vgl3* was additive, with each additional copy of the *vgl3**E allele increasing the probability of maturation. Overall, the *vgl3* effect on maturation was very similar across feed treatments and populations, except for Oulu individuals in the control-feed treatment where no apparent effect of *vgl3* was found; the observed maturation rate in this group was approximately 72% regardless of *vgl3* genotype, and there was no difference in predicted maturation probabilities between genotypes for the Oulu individuals. This relatively high maturation probability and lack of association with *vgl3* could indicate a population-specific maturation threshold linked with body condition. On average, the Oulu individuals

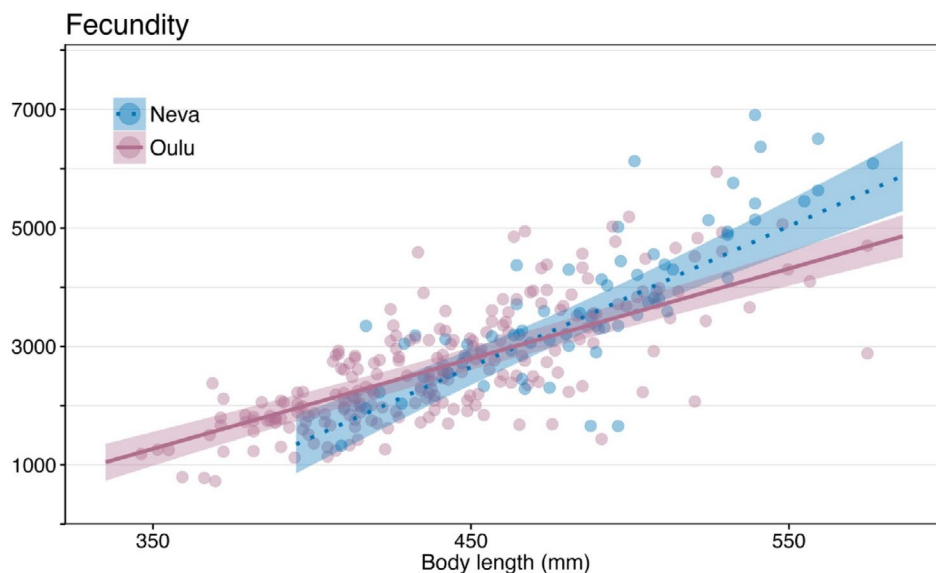


FIGURE 5 | Fecundity (number of eggs) per mature individual plotted against body length in the spring prior to spawning. The points are the observed fecundity coloured by population (blue = Neva, red = Oulu). The trendlines indicate the predicted fecundity calculated using the fecundity model. For the predictions, *vgll3* genotype was set as EL and feed as low-fat feed. Body condition was set as the mean of all the female fish included in the fecundity model. The shaded areas around the trendlines are the 95% credible intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

had lower body condition compared to Neva. If the Oulu salmon have a lower body condition threshold for maturation compared to Neva salmon, then our result could indicate that when feed energy content is sufficiently high and the individuals are able to acquire abundant energy reserves, the effect of *vgll3* on maturation is bypassed by other environmental and genetic mechanisms mediating maturation (Besnier et al. 2024). In a previous study, *vgll3* was not associated with female age at maturity in a commercial Mowi aquaculture strain in a common-garden experiment (Ayllon et al. 2019). In that study too, the authors hypothesised that excess availability of feed and other environmental conditions under farming conditions and the strain's long history of domestication, which all influence growth rate, may have overridden the potential effect of *vgll3* on maturation.

To better understand the genetic basis and adaptive potential of age at maturity in female Atlantic salmon, we calculated both heritability and *vgll3*'s contribution to phenotypic variance of maturation. Heritability of female maturation at 4 years of age was estimated to be approximately 0.295 in our study. This estimated heritability for females was lower compared to the heritability of first-time maturation for 2-year-old male salmon (estimated to be 0.68) in our experimental cohorts (Åsheim et al. 2023). Our heritability estimate of female maturation is in line with the median heritability estimate of 0.21 calculated for maturation age in multiple salmonid species where both sexes were pooled (Carlson and Seamons 2008). Sex-specific selection in salmon maturation suggests that we should expect different heritabilities for the sexes (Mousseau and Roff 1987). The approximately 40% difference between the estimated heritabilities of age at maturity for females and males from our experimental cohorts highlights the importance of accounting for sex when estimating heritabilities for traits under sex-specific selection. For such traits, inadequately accounting for sex can lead to heritability estimates that do not accurately represent either sex, thus biasing interpretations of the adaptive potential of the trait.

In addition to heritability, we calculated *vgll3*'s contribution to the phenotypic variance of first-time maturation and found the contribution to be only ~2%. In contrast, the contribution of *vgll3* to the phenotypic variance in males from the same common-garden experiment was ~13% (Åsheim et al. 2023). The lower heritability of maturation and *vgll3*'s contribution to it for females indicates that the additive genetic component of age at maturity is not as prominent in female compared to male Atlantic salmon. This smaller additive genetic contribution highlights the importance of environmental factors on female maturation in our experiment, though we cannot exclude the potential influence of nonadditive genetic factors (e.g., epistasis) on maturation (Roff and Emerson 2006). Small sample sizes prevented us from fitting animal models that could have quantified the effect, if any, of epistatic effects. The lower heritability of female maturation could be linked to age at maturity being an important life-history trait, as traits connected with fitness often exhibit lower heritabilities compared to morphological traits (Falconer and Mackay 1996; Mousseau and Roff 1987). This lower heritability of fitness-linked traits has often been attributed to smaller genetic variation (Falconer and Mackay 1996), but lower heritability can also be a consequence of higher residual variance (due to e.g., environmental and nonadditive genetic effects) for life-history traits that are expressed at an older age (Kruuk et al. 2000; Price and Schluter 1991; Wheelwright et al. 2014). In our heritability calculations, residual variance was fixed to a single value due to our modelling approach. Therefore, we do not expect residual variance to play a key role in our estimation of maturation heritability.

In Atlantic salmon, both sexes get a reproductive fitness benefit from older age at maturity (Mobley et al. 2020, 2024), and the mean sea age at maturity for the sexes can differ between populations due to local adaptation (Erkinaro et al. 2019; Persson et al. 2023; Tréhin et al. 2024). On average, however, age at maturity is likely to be higher for female salmon compared to

males, partly due to female reproductive success being more tightly linked with body size and thus, with age (Czorlich et al. 2018; Erkinaro et al. 2019; Fleming et al. 1996; Fleming and Einum 2011; Mobley et al. 2020). Interestingly, differences between the sexes in how *vgll3* influences age at maturity, where the effect of *vgll3* on age at maturity appeared to be smaller for females than for males, have also been reported for a wild Norwegian Atlantic salmon and a Baltic salmon population (Besnier et al. 2024; Miettinen et al. 2024). Moreover, in their study comparing historical and contemporary salmon samples from river Etne in Norway, Besnier et al. (2024) noted that the influence of *vgll3* on age at maturity was almost completely absent in contemporary samples from the 2010s, while an effect was still present in the samples from the 1980s. Age at maturity is mediated by multiple loci (Sinclair-Waters et al. 2020). With this polygenic nature of the trait in mind, together with the findings of the sex-specific patterns in *vgll3*'s effect on maturation in our study and in the studies of wild populations (Besnier et al. 2024; Miettinen et al. 2024), age at maturity in female Atlantic salmon might have a larger environmental component compared to males.

4.2 | Other Factors Influencing Maturation

Across taxa, individuals require sufficient energy stores for initiating the maturation process both in terms of metabolic costs and direct energetic costs allocated to offspring (Ginther et al. 2024). Total energy allocated to reproduction is similar for both sexes, but females invest proportionally more in gamete production than males (Hayward and Gillooly 2011). Similar patterns in energy allocation between sexes are also found in Atlantic salmon, where females invest approximately 60% of the energy allocated to reproduction in gonads, whereas for males the same allocation is approximately 10% (Jonsson and Jonsson 2003). Age at maturity in Atlantic salmon is often thought to be, and is modelled as, a threshold trait, where the initiation of the maturation process is triggered by an underlying (continuous) liability trait, such as growth rate, body size or somatic energy reserves, surpassing a genetically predetermined threshold value (Hutchings 2021; Lynch and Walsh 1998; Piché et al. 2008; Thorpe et al. 1998). Due to the large reproductive fitness advantage they receive from delaying maturation, female Atlantic salmon have a higher growth and body size threshold for maturation compared to males (Hutchings and Jones 1998; Jonsson and Jonsson 2011; Tréhin et al. 2021). As expected, we found both larger body size and higher body condition to be associated with a higher probability of maturation.

Though an effect of *vgll3* on body condition has been demonstrated previously in males (Debes et al. 2021; House et al. 2023), we were unable to find an association in this study in either the maturation or the body condition model. As shown by House et al. (2023) and Debes et al. (2021), body condition is not a static trait but rather changes throughout the year, and the magnitude of differences in body condition between the *vgll3* genotypes also changes depending on sampling timepoint. There are likely to be two important timepoints where the level of somatic energy reserves is evaluated against the maturation threshold: one in autumn and one in spring (Mangel and Satterthwaite 2008). We chose to measure body condition in May, as body

condition in spring and early summer is a predictor of maturation status in autumn for salmon (Kadri et al. 1997; Mangel and Satterthwaite 2008; Thorpe et al. 1998). Moreover, this is the time point where an association between *vgll3* and body condition has been previously found in males (Debes et al. 2021), though we cannot exclude the possibility that *vgll3* may influence body condition differently in females than in males.

Environmental conditions influence both the availability of energy resources and how organisms allocate the acquired energy into different functions such as growth, homeostasis and reproduction (Edward and Chapman 2011; Willmer et al. 2005). We did not find an independent effect of feed treatment on maturation probability, although diet can influence age at maturity in Atlantic salmon (Jonsson et al. 2013). We did, however, detect a possible indirect feed effect via body condition. The individuals that had been fed the lower-energy low-fat diet for approximately 2.3 years before spawning had lower body condition compared to the individuals receiving the standard, higher-energy diet. The lower body condition in the low-fat diet treatment suggests that immature individuals in this treatment were unable to acquire sufficient energy stores in the spring for maturation in the autumn due to reduced feed quality, causing them to be unable to reach the body condition threshold needed for maturation, thus delaying their maturation. The effect of diet was only found on body condition and not on body length. The lack of diet effect on body length indicates that the salmon in the higher-energy feed treatment were allocating their acquired energy to energy storage rather than to growth.

We found that the population of origin influenced body length and body condition. Individuals from the Oulu population not only had shorter body length, but they also had lower body condition compared to Neva individuals. In addition, there was an interaction between diet and population whereby Oulu individuals displayed a larger reduction in body condition in the low-fat treatment than Neva individuals. As individuals from both populations were grown in the same environmental conditions and mixed evenly between tanks and feed treatments, the observed differences indicate that there are possible genetic or epigenetic differences between the populations in their way of utilising dietary energy resources.

4.3 | Fecundity

The positive correlation between female body size and fecundity is well documented in various organisms, including fish (Barneche et al. 2018; Fleming 1996; Hanson et al. 2020; Moffett et al. 2006; Thorpe et al. 1984), reptiles (Meiri et al. 2012; Wu et al. 2022), amphibians (Lorrain-Soligon et al. 2023; Toli et al. 2024) and insects (Berger et al. 2008; Chelini and Hebets 2017; Preziosi et al. 1996). The results from this study also demonstrated this relationship between individual body size and egg number, with larger females producing more eggs. Additionally, we found that body condition in the spring prior to spawning also influenced fecundity. The individuals that had a higher body condition in the spring also produced more eggs. Both body size and body condition were found to affect fecundity in the same model, which indicates that both traits may be important for fecundity and that the mechanisms of how they

influence egg number can be different. Body condition can reflect the availability of energy resources or, alternatively, body shape (Cren 1951). Thus, body condition may represent space available for eggs, particularly the volume of the body cavity.

Oulu individuals produced fewer eggs for a given body length compared to the Neva individuals. Differences in fecundities between populations, after accounting for body size or age, have been reported for wild Atlantic salmon in Europe (de Eyto et al. 2015; Fleming 1996; Hanson et al. 2020; Klemetsen et al. 2003). This variation between rivers could arise due to the spawning history of the female (e.g., first-time vs. repeat spawner) affecting egg size and/or number (Reid and Chaput 2012) or due to environmental variation either in the freshwater or marine environment utilised by the salmon (Jacobson et al. 2021). The finding of differing fecundities between the two populations in our study indicates that beyond environmental and age-specific effects, genetic factors between populations may influence the number of eggs an individual produces. However, we did not find a clear effect of *vgll3* on fecundity, as estimated by egg number, but there was a weak interaction between population and *vgll3* on fecundity—the additive effect of *vgll3* on fecundity was weaker for Oulu compared to Neva individuals. When interpreting these *vgll3* results from the model, it should be noted that there were fewer Neva individuals in our study cohort compared to Oulu individuals and, in particular, fewer LL individuals from the Neva population (11 compared to 65 from the Oulu population included in the fecundity analysis). This could lead to an apparent effect of *vgll3* on fecundity when, in fact, it is just a statistical artefact arising from an unbalanced experimental design. The lack of a similar pattern in the observed fecundities suggests that this may be the case (Figure S4). We recommend follow-up studies to either confirm or reject this interactive effect.

4.4 | The Importance of Studying Female Atlantic Salmon Reproduction

In many species, females and males differ in their size and age at maturity (Fairbairn 2013; Stamps and Krishnan 1997), which can complicate the comprehensive study of the factors influencing maturation. Female salmon typically mature at an older age and larger size compared to males (Czorlich et al. 2018; Mobley et al. 2020) and thus, they have often been neglected in laboratory studies of maturation due to the financial, logistical, and labour costs associated with rearing the fish until maturation. The focus on male maturation may also partly be due to Atlantic salmon's major role in aquaculture. There, early maturation is a larger problem in male compared to female salmon where maturing individuals shift their energy allocation from somatic growth to gonadal development which leads to smaller body sizes and financial losses (Taranger et al. 2010). Inadvertently, the exclusion of female salmon from long-term studies of maturation in controlled settings has led to incomplete knowledge of the processes underlying age at maturity. This is despite female age at maturity being a core component of many population management models. Exploitation of many wild Atlantic salmon stocks is managed by stock-specific spawning targets based on biological reference points where these targets are expected to be set at levels that prevent overexploitation (Chaput et al. 1998;

White et al. 2023). One important reference point used for the spawning targets is the number of eggs individuals in the managed population produce (Forseth et al. 2013; O'Connell and Dempson 1995). Old and large females with high fecundity are known to have a large influence on population productivity across fish species (Hixon et al. 2014; Marshall et al. 2021). This connection between age at maturity and fecundity highlights the importance of female salmon for management and conservation, and for understanding how different factors influence age at maturity and reproductive traits in female Atlantic salmon.

4.5 | Conclusions

Understanding the nature of sex-specific variation in life-history traits is a major goal in evolutionary biology. The results of our study demonstrate that both environment and genetics contribute to maturation and reproductive traits in females. Additionally, we show that populations may differ in their response to environmental conditions and that population-level genetic background shapes life-history traits. The lower heritability of maturation in females compared to males suggests that the environment is likely more important in female maturation in this species. In the future, studies investigating life-history traits in both sexes simultaneously will be beneficial for elucidating sex-specific influences of genetics and environmental factors, as will comparisons drawn from multiple populations, as such studies may reveal population-specific factors influencing reproductive traits.

Author Contributions

C.R.P., P.V.D., K.S.M., A.H.H., E.R.Å., K.B.M.: conceptualization; E.R.Å., K.S.M.: data curation; K.S.M., R.J.O., E.R.Å.: formal analysis; C.R.P., K.S.M.: funding acquisition; K.S.M., E.R.Å., P.T.N., J.M.P., P.L., K.B.M.: investigation; P.V.D., A.H.H., K.S.M., E.R.Å., C.R.P., K.B.M.: methodology; C.R.P.: project administration; C.R.P., J.E.: resources; C.R.P., K.B.M.: supervision; K.S.M.: visualisation; K.S.M.: writing – original draft; K.S.M., C.R.P., K.B.M., E.R.Å., R.J.O., J.M.P., P.T.N., J.E., P.V.D., A.H.H.: writing – review and editing.

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Disclosure

Benefits Generated: Benefits from this research accrue from the sharing of our data and results on public databases, as described in Data Availability Statement.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code used in the analysis have been made available in Zenodo via the URL <https://doi.org/10.5281/zenodo.14921737>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.