Received: 5 December 2023 | Revised: 11 April 2024 | Accepted: 15 May 2024

DOI: 10.1111/mec.17435

ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Sex-specific overdominance at the maturation *vgll3* gene for reproductive fitness in wild Atlantic salmon

Kenyon B. Mobley[1,2] | Henry J. Barton[1] | Mikko Ellmén[1] | Annukka Ruokolainen[1] | Olavi Guttorm[1] | Hans Pieski[1] | Panu Orell[3] | Jaakko Erkinaro[3] | Craig R. Primmer[1,4]

[1]Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

[2]Department of Genetics, Norwegian College of Fishery Science, UiT the Arctic University of Norway, Tromsø, Norway

[3]Natural Resources Institute Finland (Luke), Oulu, Finland

[4]Institute for Biotechnology, Helsinki Institute of Life Science (HiLIFE), University of Helsinki, Helsinki, Finland

Correspondence
Kenyon B. Mobley, Department of Genetics, Norwegian College of Fishery Science, UiT the Arctic University of Norway, Tromsø Norway.
Email: kenyon.b.mobley@uit.no

Present address
Henry J. Barton, Genevia Technologies Oy, Tampere, Finland

Funding information
Research Council of Finland, Grant/Award Number: 302873, 307593, 327255 and 342851; H2020 European Research Council, Grant/Award Number: 101054307 and 742312

Handling Editor: Yanhua qu

Abstract

Linking reproductive fitness with adaptive traits at the genomic level can shed light on the mechanisms that produce and maintain sex-specific selection. Here, we construct a multigenerational pedigree to investigate sex-specific selection on a maturation gene, *vgll3*, in a wild Atlantic salmon population. The *vgll3* locus is responsible for ~40% of the variation in maturation (sea age at first reproduction). Genetic parentage analysis was conducted on 18,265 juveniles (parr) and 685 adults collected at the same spawning ground over eight consecutive years. A high proportion of females (26%) were iteroparous and reproduced two to four times in their lifetime. A smaller proportion of males (9%) spawned at least twice in their lifetime. Sex-specific patterns of reproductive fitness were related to *vgll3* genotype. Females showed a pattern of overdominance where *vgll3**EL genotypes had three-fold more total offspring than homozygous females. In contrast, males demonstrated that late-maturing *vgll3**LL individuals had two-fold more offspring than either *vgll3**EE or *vgll3**EL males. Taken together, these data suggest that balancing selection in females contributes to the maintenance of variation at this locus via increased fitness of iteroparous *vgll3**EL females. This study demonstrates the utility of multigenerational pedigrees for uncovering complex patterns of reproduction, sex-specific selection and the maintenance of genetic variation.

KEYWORDS
life-history, mating success, reproductive success, sexual conflict, sexual selection, trade-off

1 | INTRODUCTION

Sex-specific selection arises when males and females have discordant selection on fitness and may lead to sexual conflict (Connallon et al., 2010; Wright et al., 2018). Sex-specific selection can shape fitness, gene expression, genomic architecture and the maintenance of genetic variation (Johnston et al., 2013; Mank, 2017; Mérot et al., 2020; Wright et al., 2018). The mechanisms underlying sex-specific selection are not well understood, partly because fitness may be affected by several interacting life-history traits such as survival, growth, sexual maturation, and offspring survivorship (Mérot et al., 2020). This selection can vary through different periods of time due to spatial and temporal environmental heterogeneity (Brown & Kelly, 2018) and potentially shift during different life history stages.

Recent studies that investigate the genetic basis of sex-specific selection are beginning to shed light on the topic. For example, sex-specific selection on a single locus maintains a polymorphism in horn size of male Soay sheep (Johnston et al., 2013). Here, a life history trade-off between survival and fitness drives antagonistic pleiotropy at the locus in males. The product of this trade-off results in a pattern of overdominance, or heterozygote advantage maintaining polymorphism in the locus (Johnston et al., 2013). In the seaweed fly, *Coelopa frigida*, a chromosomal inversion polymorphism underlies a life-history trade-off between larval survival and adult reproduction. Antagonistic pleiotropy on this inversion results in a pattern of overdominance that maintains this polymorphism (Mérot et al., 2020). In Atlantic salmon, *Salmo salar*, sex-dependent dominance and sexual antagonism at a large effect locus is thought to maintain variation in maturation age (Barson et al., 2015). Yet, questions remain concerning the genetic basis of sex-specific selection in species with complex life histories. For example, how is sex-specific selection maintained in species that have multiple reproductive events in their lifetime? Moreover, what are the sex-specific fitness consequences of different reproductive strategies? These questions are particularly relevant in natural populations where selection may differ during different life stages and may mask the root causes of sex-specific selection.

Atlantic salmon is an interesting model system to investigate the nature of sex-specific selection and the link to reproductive fitness (Barson et al., 2015; Mank, 2017; Mobley et al., 2021). On average, male and female Atlantic salmon have different optimal life history strategies, including differences in maturation timing and reproductive fitness that may ultimately drive differences in reproductive optima (Mobley et al., 2020, 2021). Most Atlantic salmon populations are anadromous, whereby they reproduce in fresh water and the juveniles (parr) spend a number of years in fresh water before migrating to sea (Erkinaro et al., 2019; Jonsson & Jonsson, 2011; Mobley et al., 2021; Økland et al., 1993). Female and male parr spend similar amounts of time in fresh water before migrating to the sea (Mobley et al., 2020). However, females have a negative correlation in pre- and post-marine migration growth (Einum et al., 2002) and females that spend more time in fresh water spend less time at sea before return migrating to spawn (Erkinaro et al., 1997; Mobley et al., 2020). Atlantic salmon spend one or several years feeding and growing at sea prior to returning to fresh water to spawn (Fleming, 1996, 1998; Jonsson & Jonsson, 2011; Mobley et al., 2021). The time spent at sea prior to returning to spawn, known as sea age or sea age at maturity, is commonly measured in sea winters (SW). Males usually mature after 1SW even though reproductive fitness is higher in older and larger males (Mobley et al., 2020). Females, on the other hand, spend more time at sea prior to returning to spawn than males (Mobley et al., 2020). Females that spawn after spending only 1 year at sea have lower reproductive fitness than those that spend at least 2 years at sea (Mobley et al., 2020) demonstrating that females should delay maturation in order to maximise reproductive fitness. The optimal time spent at sea differs between male and female Atlantic salmon theoretically to maximise reproductive fitness and may represent a life-history tradeoff between maturation, reproduction and survivorship (Mobley et al., 2020, 2021). For example, high mortality in the marine phase may confer a selective advantage to earlier maturation, such that higher probability of survival before reproduction may offset the reproductive fitness advantage of being older and larger at maturity (Hard et al., 2008; Mobley et al., 2021; Thorpe, 2007).

Atlantic salmon commonly reproduce only once in their lifetime prior to death, a strategy known as semelparity. However, a small proportion of anadromous Atlantic salmon are iteroparous and may reproduce in several different years (Birnie-Gauvin et al., 2023; Bordeleau et al., 2020; Fleming, 1998; Fleming & Einum, 2011; Fleming & Reynolds, 2004; Jonsson & Jonsson, 2011; Mobley et al., 2021; Persson et al., 2023). Iteroparity, or repeat-spawning, can be advantageous in that individuals may gain additional reproductive fitness in subsequent spawning years. Iteroparous individuals are more likely to be earlier-maturing salmon that invest proportionally less into reproduction than later-maturing salmon after controlling for sea age (Aykanat et al., 2019). Iteroparity safeguards against periods of low adult recruitment (Bordeleau et al., 2020) and therefore is important for long-term population viability.

Further variation in reproductive strategies is achieved in males, as male parr may become sexually mature without a marine migration and spawn with anadromous females (Fleming, 1996; reviewed in Hutchings & Myers, 1994; Mobley et al., 2021). This phenomenon represents an alternative mating strategy in which mature male parr may gain reproductive fitness. The amount of male parr maturation and contributions to reproductive fitness is highly variable and appears to be population specific (Hutchings & Myers, 1988; Jones & Hutchings, 2002; Mobley et al., 2021).

Up to 39% of the variation in sea age for Atlantic salmon males and females is explained by a single large-effect locus, *vgll3* (vestigial-like family member 3), identified by genome-wide association mapping studies (Barson et al., 2015). The *vgll3* locus encodes a transcription cofactor involved in adipogenesis regulation in mice (Halperin et al., 2013) and influences reproductive axis gene expression in Atlantic salmon testes (Ahi et al., 2022; Verta et al., 2020). In Atlantic salmon, the *vgll3* locus is linked with body condition (fatness) (Debes et al., 2021; House et al., 2023), aerobic scope (Prokkola et al., 2022), and juvenile aggressive behaviour (Bangura et al., 2022). Alternative alleles in the *vgll3* locus are associated with either early (*vgll3**E) or late (*vgll3**L) maturation in the wild (Barson et al., 2015) and this association has been validated in controlled conditions in multiple populations (Åsheim et al., 2023; Debes et al., 2021; Sinclair-Waters et al., 2022). The *vgll3* locus exhibits incomplete sex-specific dominance that may help to explain the maintenance of variation at this locus (Barson et al., 2015). Males and females that are homozygous for the *E* allele (*vgll3**EE) most often mature after 1SW while *vgll3**LL adults mature after two or more SW (Barson et al., 2015). Due to complete dominance of the *vgll3**E allele in males, the sea age of *vgll3**EL males is similar to *vgll3**EE males, and both these genotypes return to spawn most often after 1SW (Barson et al., 2015). On the other hand, *vgll3**EL

females return to spawn at an intermediate age between both homozygotes (Barson et al., 2015). Differing phenotypic optima for males and females over sea age and body size at maturation may result in the potential for sex-specific selection and sexual conflict between the *vgll3**E and *vgll3**L alleles at the locus (Barson et al., 2015; Mank, 2017; Mobley et al., 2021). Indeed, *vgll3* alleles are maintained at intermediate frequencies in many populations (Barson et al., 2015). This may indicate that balancing selection is operating at this locus as predicted under intra-locus sexual conflict (Connallon & Clark, 2014) and is supported by simulations and empirical data (Czorlich et al., 2018; Kuparinen & Hutchings, 2019). Iteroparity is also linked to the *vgll3* locus (Aykanat et al., 2019). In particular, the odds ratio of survival until second reproduction was 2.4 times higher for *vgll3**EE compared to *vgll3**LL individuals (Aykanat et al., 2019).

In this study, we investigate sex-specific effects of the *vgll3* gene on reproductive fitness in Atlantic salmon. Differences in sea age, dominance patterns, and iteroparity at the *vgll3* locus, lead us to the prediction that alternative *vgll3* genotypes have sex-specific effects on reproductive fitness. To test this hypothesis, we reconstructed a multigenerational pedigree based on parentage assignment using single nucleotide polymorphism (SNP) data from adults and offspring collected over eight consecutive years from a population of wild Atlantic salmon from northern Finland. We then estimated reproductive success (i.e. the total number of assigned offspring) as a proxy for reproductive fitness for individual sires and dams for discrete reproductive events (i.e. spawning in different years).

We first investigated whether there were sex differences in reproductive success, iteroparity and the maximum number of reproductive events. To measure the overall contributions of the *vgll3* locus on reproductive success, we tested for a sex-specific relationship between specific *vgll3* genotypes on the cumulative number of offspring over all reproductive events (total reproductive success) and for first reproductive event (age at first reproduction). We also compared reproductive success of semelparous and iteroparous individuals in the first reproductive event to see whether there was a sex-specific reproductive advantage to spawning earlier. In this manner, we can ascertain whether there was a fitness advantage between these two life-history strategies mediated by the *vgll3* locus. Finally, we test additive and dominance models of *vgll3* genotypes on reproductive fitness for each sex separately to help understand the nature of sex-specific selection. The combined goal of these investigations is to understand the effect of sex-specific selection and the underlying genetic architecture on reproductive fitness in a species under natural conditions.

2 | METHODS

The lower Utsjoki sampling site is located at the mouth of the Utsjoki tributary of the Teno River in northern Finland (69°54′28.37″ N, 27°2′47.52″ E) (Mobley et al., 2019). The Utsjoki River is one of the largest tributaries of the Teno River system (length, 66 km; catchment area, 1652 km^2), draining into the Teno main stem 108 km from the Barents Sea. The lower Utsjoki harbours several distinctive spawning grounds (approximately 150–400 m long), which are separated by 150- to 600-m river sections with pools and slow flowing reaches (Mobley et al., 2019). Wetted widths of the spawning areas vary from 30 to 50 m, and the maximum spawning site depth is ~300 cm, although most nests (redds) are at depths between 70 and 150 cm (Mobley et al., 2019).

Anadromous adults were sampled in September–October 2011–2018 from the lower Utsjoki River, approximately 1–2 weeks before the commencement of spawning. Adults were collected using gill nets ~1 km upstream from the Teno river mainstem in a deep pool formed from the bend in the riverbed (Mobley et al., 2019). Adults were sexed, weighed (kg) and total length (cm) was recorded. Adults were tagged with a unique alphanumeric-coded anchor dart tag in the musculature at the base of the dorsal fin. Scales were collected for age determination (see age determination below) and a small piece of the adipose fin was collected for genetic analysis prior to release near the site of capture.

Juvenile parr were sampled by electrofishing shallow areas along a 2-km tract of the lower Utsjoki River ~1 km upstream and downstream of the adult collection area in September 2012–2019 (Mobley et al., 2019). Regions with both high and low juvenile density were sampled each year to ensure sampling of offspring produced by individuals spawning in different quality habitats (Mobley et al., 2019). Parr were assigned an age class (0+, 1+, 2+ and 3+) based on total length distributions that correspond to their age in years since hatching. Parr were age classed as follows: 0+: <6 cm, 1+: 6–9 cm, 2+: 9–11.5 cm and 3+ >11.5 cm. To track yearly cohorts, only 0+ parr were collected in 2012, 0+ and 1+ were collected in 2013, 0+, 1+ and 2+ were collected in 2014, and from 2015 onward all parr were collected. Total length was measured, and scale samples were collected on a few 0+ and 1+ individuals and all 2–3+ class individuals from 2014 forward to verify age as determined by scale analysis. Parr sexual maturity was determined on all larger individuals sampled in the field from 2014 onwards. Individuals that expressed seminal fluid after stripping were considered mature male parr. Genetic samples were collected from all parr by removing a small piece of adipose and/or anal fins, after which parr were immediately returned to the river (Mobley et al., 2019, 2020).

2.1 | Age determination

Freshwater age, defined as the number of years spent in fresh water prior to migrating to sea, and sea age, defined as the number of years an individual overwintered at sea before returning to spawn, was determined for adults sampled on the spawning ground using scale growth readings as outlined in Aykanat et al. (2015) and Erkinaro et al. (2019). Hatch year (i.e. the year when alevins

hatched from eggs) for adults was then calculated as year of collection − (freshwater age + sea age). A small proportion of adults were missing scales and/or age could not be determined for all life history stages. For adults that did not have sea age ($n = 11$), sea age was interpolated using the means of sea age regressed on weight for each sex separately (Mobley et al., 2019). For adults that did not have freshwater age ($n = 53$) due to either missing scales or inconclusive scale analysis, it was assumed that freshwater age was 4 reflecting the means of freshwater age of adult males and females (females: mean 3.52 ± 0.06, males: mean 3.53 ± 0.02). Hatch year of parr was calculated as the year of collection minus the age class (0+ = same year, 1+ = −1, 2–3+ = −2). Because parr were sampled as a combined class 2–3+ for years 2018 and 2019, 2+ and 3+ individuals were pooled for each year and assumed to have a hatch year = year of collection −2. Individuals that show previous returns as adults to fresh water based on scale data were considered iteroparous.

The life history strategy of each adult is characterised by a combination of freshwater age and sea age. For example, an individual that spent 4 years in fresh water and 1 year at sea before returning to spawn would be designated as 4–1. Iteroparous individuals have an additional designation first spawning (S) and reconditioning period at sea (variable number of years). Therefore, an individual 4-1S1 would have first spent 4 years in fresh water, spawned after spending 1 year at sea, and then would have returned 2 years later to spawn a second time.

2.2 | DNA extraction and SNP genotyping

DNA extraction was carried out according to protocols outlined in Mobley et al. (2019). Genotyping was accomplished using a 176 single nucleotide polymorphisms (SNPs) of a panel originally described in Aykanat et al. (2016) with modifications to enable sequencing using Illumina platform (MiSeq or Next-Seq) sequencers (Aykanat et al., 2020). Five loci were removed from the final analysis due to high linkage ($r > 0.5$) using the LD function in the 'genetics' package (Warnes, 2012) in R (R Core Team, 2022) (Table S1). Two additional loci were excluded due to low sequencing success (>40% missing data: TN_423, 58%; TN_1088, 45%). The remaining 169 SNPs were filtered to remove individuals with low SNP coverage (>5% missing genotypes).

The *vgll3* locus was scored using the $vgll3_{TOP}$ SNP (Aykanat et al., 2020; Barson et al., 2015) and sex was determined by estimating read counts of the sex determining region, *sdY* locus, using a read-depth threshold to distinguish males (high read number) and females (low read number) (Aykanat et al., 2016, 2020).

Duplicate genotypes were identified with SEQUOIA version 1.3.3 (Huisman, 2017) and removed prior to parentage analyses. Of the duplicated genotypes, seven were adult males recaptured in a later year (confirmed by tag ID), six were parr recaptured as adults, 21 were parr recaptured in the same year, 68 were parr recaptured in different years and nine were collection or DNA extraction errors (i.e. identical genotypes in consecutive samples).

2.3 | Parentage analysis

Parentage was determined with SEQUOIA to reconstruct a maximum-likelihood, multigenerational pedigree from SNP genotypes, sex and back-calculated hatch years. The sex determining locus, *sdY* (SDY_ion2), was used for sex assignment. Parentage analysis was conducted using three methods: (1) program defaults, (2) informed parentage with priors set to zero for age at maturity of 0–1 for males and 0–3 for females, and (3) conservative parentage where all priors <0.1 set to zero to exclude all the most improbable relationships. Age structure was based on back-calculated hatch dates such that offspring cannot be assigned to individuals prior to their hatch year. Sampled parr and adults could be assigned as sires/dams and/or offspring.

2.4 | Reproductive fitness

Reproductive fitness was quantified as reproductive success, or the number of offspring assigned to a sire or dam. We determined how many reproductive events (i.e. how many different years an individual spawned) and the reproductive success of each reproductive event by grouping offspring assigned by parentage into discrete hatch years based on back-calculated hatch year of offspring. Results were then visualised, and reproductive events were identified based on the large number of offspring assigned to a particular hatch year. Assigned offspring that fell between reproductive events were assumed to be incorrectly assigned to an age class and were grouped with the first reproductive event or, in the case of iteroparous individuals, grouped with the proceeding reproductive event. The first reproductive event for each sire and dam was calculated as the first reproductive event identified by parentage. Iteroparous sires and dams were either assigned a first reproductive event corresponding to the first spawning year identified by scale analysis or by the first reproductive event identified by parentage. No individual offspring was assigned to more than one reproductive event.

2.5 | Comparison of parentage analysis methods

To assess the performance of the three parentage methods, we compared the age at first reproduction of adults to the age of first reproduction of parr assigned as parents. Age at first reproduction was calculated as the hatch year of the parent − hatch year of assigned offspring and were considered adults if age at first reproduction was >4. Sires that had an age of first reproduction ≤3 years were considered mature male parr. We used the conservative method of parentage analysis due to some cases of unrealistic assignments in the

default and informed parentage analysis methods (Supplementary Information, Figure S1).

2.6 | Statistical analyses

We constructed two datasets to test the sex-specific effects of *vgll3* genotype on reproductive fitness: (1) total reproductive success was calculated as the sum of all offspring assigned to an adult across all reproductive events and (2) reproductive success for each adult's first reproductive event. In addition, we partitioned the first reproductive event into iteroparous individuals (respawners with offspring in more than one reproductive event) and ostensibly semelparous individuals with only one known reproductive event.

A χ^2 test was employed to test for differences in the frequencies in offspring age class assigned by parentage between dams and sires.

Linear models were constructed using in the MASS package in R (Venables & Ripley, 2002) to investigate sex differences in freshwater age, sea age, sea age and body length, and sea age and body weight in sampled adults. Linear models were also used to test for differences in body length and scale age between immature male, immature female and mature male parr in the 2–3+ age class. Linear models were also used to test for sex differences in sea age and *vgll3* genotypes for (1) adults collected on the spawning ground and (2) sires and dams assigned with the conservative method of parentage analysis.

A generalised linear model (GLM) was constructed to test for differences in total reproductive fitness between the sexes with respawner (semelparous/iteroparous) and the maximum number of reproductive events as factors. All GLM models of reproductive success were run with a negative binomial error distribution and a log link function based on variance distributions of model residuals in the MASS package in R (Venables & Ripley, 2002).

To test for differences in sex-specific effects of the *vgll3* gene on reproductive success, negative binomial GLMs were constructed with reproductive fitness as the response variable and *vgll3* genotype as a fixed effect. Reproductive success increases with sea age (Mobley et al., 2019, 2020) and therefore sea age was included in the models as a covariate. Body size (body length and body weight) are highly correlated with sea age (Mobley et al., 2020) but were not included in the models as these measures were only available for adults at the time of sampling whereas sea age could be back calculated for all potential sires and dams.

Generalised linear models were run for sires and dams separately using the restricted dataset to compare the differences in reproductive success in the first reproductive event. The restricted dataset excluded sires and dams that had offspring assigned in reproductive events prior to 2011 (the first year of the time series) since only adults were assigned as offspring. Similarly, sires and dams that had their first reproductive event after 2017 (the second last year of the time series) were not included as these would only include offspring of 0+ and 1+ age classes and therefore offer an incomplete estimate of reproductive fitness.

To investigate whether *vgll3* genotype influenced reproductive fitness of iteroparous compared to semelparous individuals, negative binomial GLMs were constructed with reproductive success as a response variable, *vgll3* genotype and respawner as fixed effects and sea age as a cofactor. Models were run for sires and dams separately using the restricted dataset to compare the differences in reproductive success in the first reproductive event.

To test whether *vgll3* genotype conformed to additive and/or dominance effects, a negative binomial GLM was fitted with additive (i.e. *vgll3**EE = 1, *vgll3**EL = 0 and *vgll3**LL = −1; continuous covariate) and dominance (i.e. *vgll3**EE & *vgll3**LL = 0 and *vgll3**EL = 1; continuous covariate) effects on reproductive success with sea age as a covariate (Niemelä et al., 2022; Xiang et al., 2018) using the restricted dataset. We included both additive and dominance effects to estimate whether there are dominance effects on top of additive effects (Xiang et al., 2018).

All statistical models were performed in R (R Core Team, 2022). Interactions were first tested and removed if non-significant ($\alpha = 0.05$). Model fits were assessed by inspecting residual plots (i.e. normal Q-Q plots, standardised versus fitted residuals and histograms) using the DHARMa version 0.4.5 package (Hartig, 2022). All means are reported ± one standard error of the mean.

3 | RESULTS

A total of 685 adult Atlantic salmon (93 females, 592 males, Figure S2), and 18,265 juvenile parr (Figure S3) were sampled over the 8 years. All adults and 18,172 parr were genotyped using the SNP panel. After filtering and removal of duplicate genotypes, 632 adults (86 females and 546 males) and 16,175 parr were used for parentage analysis. Using the conservative parentage dataset, 8176 offspring (50.5%) were assigned to at least one parent. A total of 4276 offspring were assigned to dams, 5954 offspring were assigned to sires, and 2054 offspring were assigned to both dams and sires. A total of 97 females were assigned as dams, 77 sampled as adults and 20 sampled as parr. A total of 337 males were assigned as sires, 301 sampled as adults and 36 sampled as parr (Table S2).

Parentage analysis demonstrated that 78.9% of offspring assigned to sires and dams were from the 0+ age class, 16.4% from the 1+ age class, 3.8% from the 2–3+ age class and 0.9% were resampled adults (Figure S4). The distribution of offspring in age classes did not significantly differ between those assigned to dams and sires ($n = 10{,}230$, $\chi^2 = 1.435$, df = 3, $p = .697$, Figure S4).

3.1 | Sampled adults

On average, freshwater age was similar for adult females and males based on scale readings (females = 3.52 ± 0.06, range 3–5 years; males = 3.53 ± 0.03, range 3–6 years; freshwater age ~ sex(male): estimate = 3.519 ± 0.066, $t = 0.102$, $p = .919$). However, females spent significantly more years at sea before returning to spawn for the first

time (females = 2.34 ± 0.08, range 1-4SW; males = 1.29 ± 0.03, range 1-4SW; sea age ~ sex(male): estimate = −1.057 ± 0.074, $t = -14.290$, $p < .001$). Body size of sampled adults was highly correlated with sea age and the relationships were sex-specific (sea age ~ ln body length (cm) * sex(male): estimate = −1.979 ± 0.256, $t = -7.716$, $p < .001$; sea age ~ ln weight (kg) * sex (male): estimate = −0.464 ± 0.081, $t = -5.732$, $p < .001$).

Twenty-six sampled individuals (13 females and 13 males) were identified as iteroparous by scale aging analysis. The mean sea age at first maturity of these iteroparous females was 2.38 ± 0.24 *SE* (range 1–3 SW) at the time of first spawning. The mean sea age at first maturity of iteroparous males was 1.08 ± 0.08 *SE* (range 1–2 SW) at the time of first spawning. All iteroparous sampled individuals had a 2-year gap between the first and second reproductive events.

3.2 | Mature male parr

A total of 41 mature male parr were collected in 2014–2019 accounting for 9.3% (± 2.3) of male parr in the 2–3+ age class and 1.7% (± 0.1) of all parr per year. Mature male parr ranged from 2 to 3 years with a mean of 2.25 ± 0.08 based on scale data ($n = 28$) (Figure S5). Mature male parr were significantly older and larger than immature male and female parr in the 2–3+ age class (female vs. immature male parr scale age (years): estimate = 0.002 ± 0.018, $t = 0.097$, $p = .923$; female vs. mature male parr scale age (years): estimate = 0.207 ± 0.043, $t = 4.790$, $p < .001$; female vs. immature male parr length (cm): estimate = 0.022 ± 0.107, $t = 0.203$, $p = .839$; female vs. mature male parr length (cm): estimate = 1.025 ± 0.262, $t = 4.289$, $p < .001$; Figure S5).

3.3 | Parentage analysis

A large proportion of adult females (89.5%) and males (61.7%) sampled that were successfully genotyped had offspring assigned by parentage analysis. Assigning offspring to discrete reproductive events based on back-calculated hatch dates demonstrated that 1.4% (62/4276) of offspring assigned to dams and 1.3% (77/5954) of offspring assigned to sires were not assigned to a reproductive event. These offspring were assigned to the proceeding reproductive event.

The most common life history strategies for semelparous females was 3–2 and 4–2 (Figure S6). Parentage analysis identified 26% of adult females spawned in multiple years, with at least one dam spawning in up to four reproductive events and two dams that spawned in three reproductive events (Figure 1). The reproductive events of iteroparous females were commonly 2 years apart. Other iteroparous dam spawning patterns included a pause between spawning that were 3 (3 dams) and 5 (1 dam) years between reproductive events.

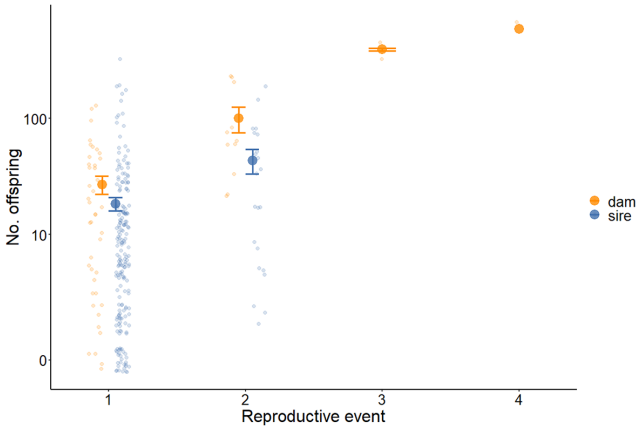

FIGURE 1 The relationship of total reproductive success (no. offspring) and the maximum number of reproductive events for individual sires and dams. Sires and dams that have one reproductive event are semelparous while sires and dams that had >1 reproductive event were iteroparous. Large circles with error bars represent the mean ± *SE*, while small circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis and the *y*-axis for reproductive fitness is $\log_{10}$-transformed.

The most common life history strategy for semelparous sires was 3–1 and 4–1 (Figure S6). A smaller percentage of sires (9%) spawned multiply compared to females (Figure 1). Repeat spawning patterns for iteroparous sires also showed a common 2-year period between reproductive events. Additionally, the reproductive events of iteroparous sires were 3 years (3 sires), 4 years (1 sire) or remarkably, 7 (1 sire) years apart. Seven adult males lacking repeat spawning information from scale data had offspring >1 year before they were sampled based on parentage analysis. Two of these males were 3SW males with many offspring consistent with a repeat spawning pattern of 1S1. One additional 3SW male sampled in 2011 had one adult offspring consistent with a 1S1 repeat spawn pattern. These three males were therefore considered 1S1. The remaining four adult males that lacked scale data had a repeat spawning pattern of 0S1, or maturation <1SW and may represent offspring sired as mature male parr. However, these four males were assumed to have a freshwater age of 4 years and may only have spent 3 years in fresh water. Offspring sired by these males amounted to five offspring.

A negative binomial GLM investigating the relationship between sex, iteroparity, and the maximum number of reproductive events on total reproductive success demonstrated that dams had significantly more offspring than sires and that total reproductive success increased with the number of reproductive events. However, whether a parent was semelparous or iteroparous did not significantly influence this relationship (Figure 1, Table 1).

The contributions of mature male parr to reproductive success was low, ranging from 0.05 to 2.56% of offspring sired, depending on the parentage analysis method (Table S3). Using the conservative parentage analysis method, only three offspring were

potentially sired by sampled adult males that may have spawned as mature male parr. No offspring were assigned to sampled male parr (Table S3).

TABLE 1 Results of negative binomial GLM showing the effect of sex, whether the parent was iteroparous (respawner), and the maximum number of reproductive events on total reproductive success.

	Estimate	*SE*	*Z* value	Pr(>|z|)
(intercept)	2.0127	1.1125	2.809	0.0704
Sex	−0.4544	0.1840	−2.470	**0.0135**
Respawner	0.2144	0.5983	0.358	0.7201
Reproductive event	1.1986	0.5072	2.363	**0.0181**

Note: Reference sex is female, reference respawner is iteroparous. Significance for bold values indicates α = 0.05.

TABLE 2 Results of linear models showing the effects of sex and *vgll3* genotype on sea age at first reproduction.

	Estimate	*SE*	t value	Pr(>|t|)
Adults sampled				
(intercept)	2.0727	0.0799	25.940	**<0.0001**
Sex	−0.9394	0.0673	−13.960	**<0.0001**
*vgll3**EL	0.0431	0.0584	0.738	0.4610
*VGLL3**LL	0.7915	0.0744	10.633	**<0.0001**
Parentage				
(intercept)	2.0390	0.1258	16.213	**<0.0001**
Sex	−0.8817	0.1026	−8.590	**<0.0001**
*vgll3**EL	0.0572	0.1088	0.526	0.5990
*VGLL3**LL	0.7561	0.1300	5.717	**<0.0001**

Note: Separate models were run on adults sampled dataset and dams and sires using the conservative parentage dataset. Reference sex is female, reference *vgll3* genotype is *vgll3**EE. Significance for bold values indicates α = 0.05.

3.4 | Reproductive fitness and the vgll3 locus

Sea age at first reproduction was strongly influenced by sex and the *vgll3* locus. A GLM showed significantly higher sea age at first reproduction in females and in *vgll3**LL genotypes (Table 2, Figure 2). These results were similar in both sampled adults and in adult sires and dams identified through parentage analysis (Table 2, Figure 2).

Results of GLMs on reproductive fitness demonstrated that dams possessing the *vgll3**EL genotype had three times more total offspring than either *vgll3**EE or *vgll3**LL dams (mean offspring *vgll3**EE: 33.1 ± 12.5; *vgll3**EL: 95.3 ± 24.8; *vgll3**LL: 27.1 ± 5.9, Table 3, Figure 3). However, the relationship of sea age on total reproductive success was not significant (Table 3, Figure 3). Sires, on the other hand, showed no significant relationship between total reproductive success and *vgll3* genotype after controlling for sea age. Despite this, sires possessing the *vgll3**LL genotype had two times more total offspring than either *vgll3**EE or *vgll3**EL sires after controlling for sea age (mean offspring *vgll3**EE: 14.1 ± 2.6; *vgll3**EL: 19.2 ± 5.5; *vgll3**LL: 40.3 ± 10.0, Table 3, Figure 3). Sires showed a significant relationship of total reproductive success with sea age demonstrating that older and larger sires had more offspring (Table 3, Figure 3). When linear models were restricted to offspring from just the first reproductive event, no effect of *vgll3* genotype on reproductive success was found in either dams or sires after controlling for sea age (Table 3, Figure 3). Rather, a significant positive effect of sea age on reproductive fitness was found in dams and sires (Table 3, Figure 3).

Comparing the first reproductive event between semelparous and iteroparous dams and sires revealed no effect of *vgll3* genotype after controlling for sea age (Table 4, Figure 4). However, a significant positive effect of sea age on reproductive success was apparent in sires but not in dams (Table 4, Figure 4).

Dominance effects of the *vgll3* genotype on total reproductive success were significant in dams but not in sires after controlling for sea age (Table 5). In these models of total reproductive success,

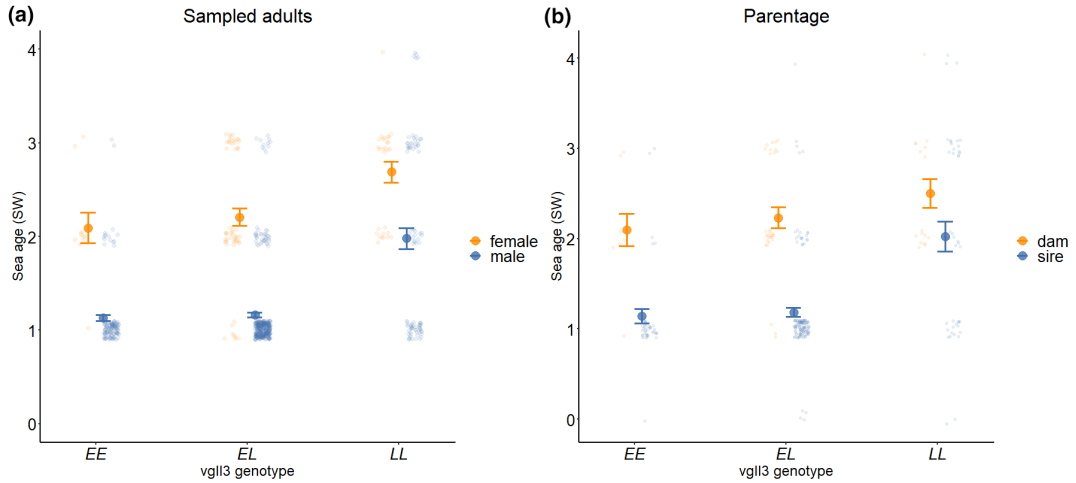

FIGURE 2 The relationship between sea age at first reproduction (sea winters, SW) and $vgll3_{TOP}$ genotype for (a) sampled adults and (b) dams and sires assigned offspring by parentage analysis. Large circles with error bars represent the mean ± *SE*, while small circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis.

TABLE 3 Results of negative binomial GLMs showing the effect of *vgll3* genotype and sea age on total reproductive success and reproductive success of the first reproductive event.

	Total				First reproductive event			
	Estimate	*SE*	*Z* value	Pr(>|z|)	Estimate	*SE*	*Z* value	Pr(>|z|)
Dams								
(Intercept)	2.7173	0.6818	3.985	**<0.0001**	2.4222	0.5708	4.243	**<0.0001**
*vgll3**EL	1.0557	0.4432	2.382	**0.0172**	0.3131	0.3705	0.845	0.3980
*vgll3**LL	−0.3245	0.5008	−0.648	0.5169	−0.4610	0.4189	−1.101	0.2711
Sea age	0.3470	0.2682	1.293	0.1958	0.4628	0.2246	2.061	**0.0393**
Sires								
(Intercept)	1.9360	0.2235	8.664	**<0.0001**	1.3977	0.2113	6.614	**<0.0001**
*vgll3**EL	0.2174	0.2072	1.049	0.2940	0.2444	0.1957	1.249	0.2120
*vgll3**LL	0.2618	0.2721	0.962	0.3360	0.0965	0.2572	0.375	0.7070
Sea age	0.6250	0.1146	5.454	**<0.0001**	0.8510	0.1079	7.891	**<0.0001**

Note: Separate models were run on adults sampled dataset and dams and sires using the conservative parentage dataset. Reference *vgll3* genotype is *vgll3**EE. Significance for bold values indicates α = 0.05.

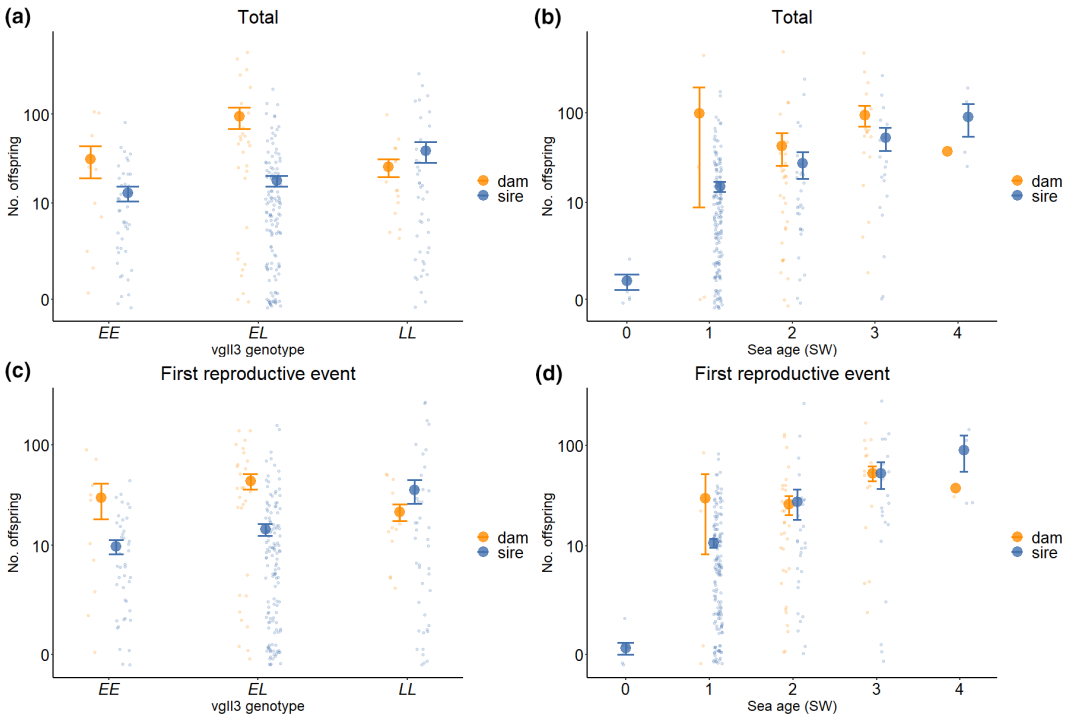

FIGURE 3 The relationship between reproductive fitness (number of assigned offspring) and $vgll3_{TOP}$ genotype and sea age at first reproduction (sea winters, SW) for dams and sires. (a) Total reproductive success and *vgll3* genotype, (b) total reproductive success and sea age, (c) reproductive success of the first reproductive event and *vgll3* genotype using the restricted dataset, (d) reproductive success of the first reproductive event and sea age (SW) using the restricted dataset. Large circles with error bars represent the mean ± *SE*, while small circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis and the *y*-axis for reproductive fitness is $\log_{10}$-transformed.

sires, but not dams, showed a significant relationship to sea age and total reproductive success (Table 5). When just limiting these models to the first reproductive event, dominance in the *vgll3* genotype was still apparent among dams but at a marginal level after controlling for sea age (Table 5). Males, on the other hand, showed no additive or dominance effects but show a significant effect of sea age on reproductive success (Table 5).

4 | DISCUSSION

The goal of this study was to study sex-specific selection on a gene linked to a life-history trait in a natural population. Reproductive fitness data of over 8000 offspring assigned to >600 parents over eight cohort years revealed that selection on female reproductive

fitness is consistent with a pattern of overdominance, or heterozygote advantage at the *vgll3* locus, among female Atlantic salmon. This pattern is driven by a higher proportion of *vgll3**EL iteroparous females contributing to reproductive fitness compared to homozygous females. Males, on the other hand, show a pattern consistent with directional selection on sea age mediated by *vgll3*, as sea age and *vgll3* genotype covary in Atlantic salmon (Aykanat et al., 2019; Barson et al., 2015; Czorlich et al., 2018; Sinclair-Waters et al., 2020). Males with *vgll3**LL genotypes mature at older ages and larger sizes and show a two-fold higher reproductive fitness than male *vgll3**EE and *vgll3**EL genotypes which have similar sea age and reproductive fitness. Previous studies have shown that sex-specific selection and patterns of overdominance maintains polymorphism in traits associated with reproduction (Johnston et al., 2013; Mérot et al., 2020; Wright et al., 2018) and it has been previously suggested for the sea age-*vgll3* association in salmon also (Barson et al., 2015). Our results indicated it is indeed highly likely that sex-specific selection on reproductive fitness at the *vgll3* locus contributes to the maintenance of variation at this locus. Interestingly, *vgll3* variation tended to explain little of the variation in reproductive fitness once sea-age variation was accounted for, suggesting that the influence of *vgll3* on sea age at maturity appears to be the main route by which *vgll3* is expected to influence reproductive fitness.

Previous studies have provided evidence that the strength of sex-specific effects of the *vgll3* locus may vary between populations, even within the same river catchment. For example, Czorlich et al. (2018) demonstrated that selection at sea against *vgll3**LL genotype individuals acts primarily on males in the same genetic population studied here (Tenojoki), but on females in another genetically-distinct population (Inarijoki) within the Teno River

TABLE 4 Results of negative binomial GLMs showing the effect of *vgll3* genotype, sea age and whether the parent was iteroparous (respawner) on reproductive success of the first reproductive event.

	Estimate	*SE*	*Z* value	*Pr*(>|*z*|)
Dams				
(Intercept)	3.0555	0.6928	4.411	**<0.0001**
Respawner	−0.5663	0.3185	−1.778	0.0754
*vgll3**EL	0.1823	0.3654	0.499	0.6178
*vgll3**LL	−0.5000	0.4089	−1.223	0.2215
Sea age	0.3938	0.2269	1.736	0.0826
Sires				
(Intercept)	1.1444	0.3040	3.764	**<0.0001**
Respawner	0.2938	0.2495	1.178	0.2390
*vgll3**EL	0.2490	0.1953	1.275	0.2023
*vgll3**LL	0.1235	0.2570	0.480	0.6310
Sea age	0.8344	0.1079	7.733	**<0.0001**

Note: Separate models were run for dams and sires using the restricted dataset. Reference respawner is iteroparous, reference *vgll3* genotype is *vgll3**EE. Significance for bold values indicates α = 0.05.

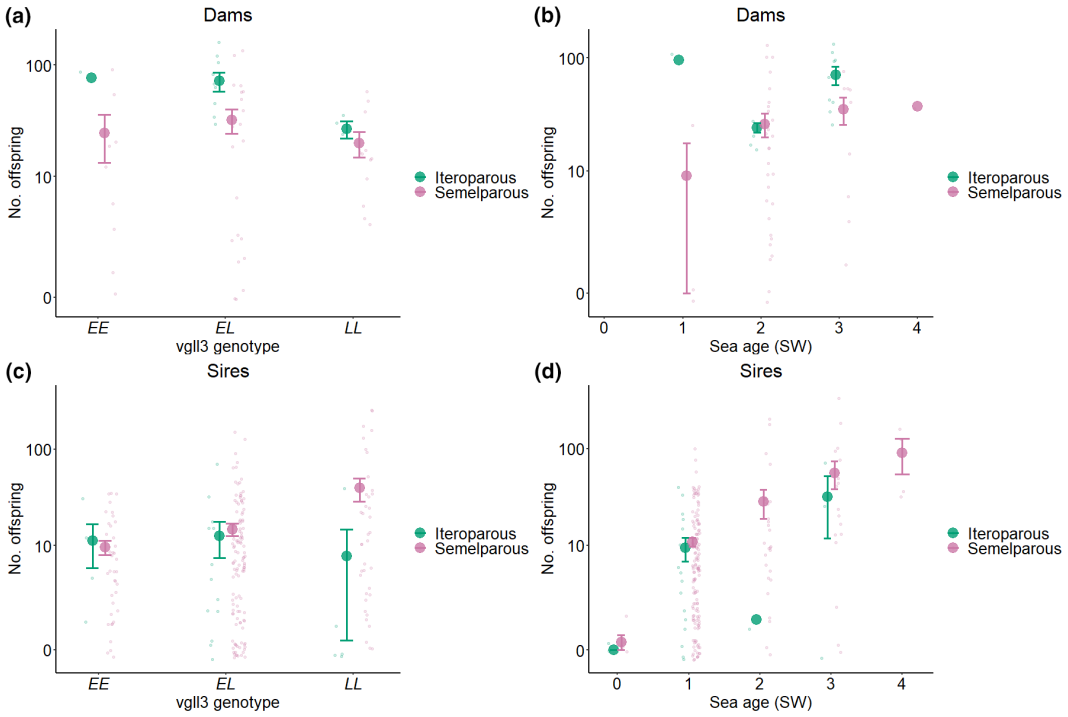

FIGURE 4 The relationship between reproductive success (number of assigned offspring) and $vgll3_{TOP}$ genotype and for dams and sires for the first reproductive event using the restricted dataset. Panels depict total reproductive success and (a) *vgll3* genotype for dams, (b) sea age for dams, (c) *vgll3* genotype for sires, (d) sea age for sires. Iteroparous (respawner) individuals are shown in green, semelparous (single spawner) individuals are shown in purple. Large circles with error bars represent the mean ± *SE*, while small circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis and the *y*-axis for reproductive fitness is $\log_{10}$-transformed.

TABLE 5 Results of negative binomial GLM models showing the effect of additive and dominance effects of *vgll3* genotype and sea age on total reproductive success and reproductive success of the first reproductive event using the restricted dataset.

	Total				First reproductive event			
	estimate	*SE*	*Z* value	Pr(>|z|)	Estimate	*SE*	*Z* value	Pr(>|z|)
Dams								
(Intercept)	2.5550	0.6643	3.846	**0.0001**	2.1917	0.5567	3.937	**<0.0001**
vgll3 additive	0.1623	0.2504	0.648	0.5169	0.2305	0.2094	1.101	0.2711
vgll3 dominance	1.2180	0.3292	3.700	**0.0003**	0.5436	0.2755	1.973	**0.0485**
Sea age	0.3470	0.2682	1.293	0.1958	0.4628	0.2246	2.061	**0.0393**
Sires								
(Intercept)	2.0669	0.2221	9.306	**<0.0001**	1.4460	0.2104	6.872	**<0.0001**
vgll3 additive	−0.1309	0.1361	−0.962	0.3360	−0.0483	0.1286	−0.375	0.7070
vgll3 dominance	0.0865	0.1685	0.513	0.6080	0.1962	0.1591	1.233	0.2180
Sea age	0.6250	0.1146	5.454	**<0.0001**	0.8510	0.1079	7.891	**<0.0001**

Note: Additive effects were coded as *vgll3**EE = 1, *vgll3**EL = 0, *vgll3**LL = −1, Dominance effects were coded as *vgll3**EE = 0, *vgll3**EL = 1, *vgll3**LL = 0. Significance for bold values indicates α = 0.05.

catchment. This difference in selection is hypothesised to be due to differences in genetic architecture including the strength of allelic effects and sex-dependent dominance (Czorlich et al., 2018). Notably, the Tenojoki population had a male-biased sex ratio whereas in the Inarijoki population the sex ratio was closer to parity (Czorlich et al., 2018). In our study, a highly male-biased sex ratio in adults signifies that females are the limiting sex and limits male reproduction (Andersson, 1994; Emlen & Oring, 1977). In addition, a larger proportion of sampled adult females reproduced and a relatively high proportion of females (26%) were iteroparous compared to males (9%) indicating that females are indeed limiting at this location.

Iteroparity in salmonids has been proposed as an evolutionary trade-off for reproductive fitness in their first reproduction for future reproductive benefits (Bordeleau et al., 2020; Christie et al., 2018; Persson et al., 2023). In general, iteroparous individuals have higher lifetime reproductive fitness than semelparous individuals (Christie et al., 2018; Seamons & Quinn, 2010). However, semelparous spawners in some salmonid species may have higher reproduction in the first reproduction than iteroparous individuals (Christie et al., 2018). Based on the comparison of reproductive fitness within the first reproductive event, there appears to be no reproductive fitness advantage to iteroparity compared to semelparity mediated by the *vgll3* locus in either dams or sires after sea age at maturity is taken into account. Rather, the increased likelihood of survival of *vgll3**EL females to iteroparity may help to explain the advantage of iteroparity in Atlantic salmon.

Atlantic salmon have remarkable diversity in life history patterns (Erkinaro et al., 2019; Harvey et al., 2022; Mobley et al., 2021; Persson et al., 2023). Previous studies in the Teno River have uncovered 120 different combinations of freshwater age, sea age, and repeat spawning patterns based on scale information (Erkinaro et al., 2019). In this study, 27 unique life history strategies were uncovered using combined information from scale data and parentage analysis from a single spawning ground in the Teno River. Sixteen of the unique life history strategies were based on scale data alone, while the remainder were only revealed following reconstructing patterns of multiple mating based on genetic parentage analysis. Thus, we demonstrate how scale analysis combined with genetic parentage analysis uncovered complex repeat spawning behaviour of Atlantic salmon that would otherwise go unrecognised based on scale data alone. For example, several iteroparous individuals identified through parentage analysis did not have signatures of repeat spawning in scale readings indicating that scale-readings alone likely underestimate iteroparity and thus the overall life-history diversity in this system may be even higher than previously thought. Additionally, several individuals had unusually long gaps between spawning events as deduced from parentage analysis. It is possible that individuals that had greater than 4 years between spawning events may have skipped spawning entirely during this period, spawned in different locations in the interim, or returned to spawn on their natal spawning ground but were either unsuccessful or no offspring were sampled. Extending the time frame of the study, increasing sampling locations and/or increasing sampling effort may help to clarify genetic relationships between offspring and iteroparous adults.

Mature male parr occur commonly in Atlantic salmon populations although their contribution to reproductive fitness is unknown in most cases (Mobley et al., 2021). It is estimated that between 0 and 25% of ≥1-year-old parr may be mature males in the Teno River system (Heinimaa & Erkinaro, 2004). Previous investigations using microsatellite markers on four cohort years identified limited potential for mature male parr to contribute to reproductive fitness in the Utsjoki river mouth population (Mobley et al., 2019, 2020). In this study, we found a small (9.3) percentage of mature male parr among 2- to 3-year-old parr sampled in the field. These mature male parr had an age at maturity between 2 and 3 years and were significantly older and larger than immature males of the same age classes, based on scale readings. Because

no mature male parr were resampled as adults, we used a minimum of 3 years of age at maturation as a cutoff for mature male parr. Using this method, we reduced the potential for ascribing parentage to males that may have matured after 3 years in fresh water which was the second most common life history pattern in males (i.e. 3–1). Our analysis identified no offspring sired by mature male parr including those that were identified as mature male parr in the field, and only three offspring potentially sired as mature male parr from adults collected in the field. These results strongly suggest that the contribution of mature male parr to reproductive fitness is negligible in this system. Because the mature male parr were larger than immature male parr of the same age class, it is possible that additional mature male parr may have been present but were either not sampled because they escaped electrofishing, were in deeper inaccessible sections of the river, or had migrated to other parts of the river system (Erkinaro et al., 1998; Erkinaro & Niemelä, 1995). Therefore, there remains some uncertainty with estimating the contributions to mature male parr based on current available data, but it is unlikely to be significant.

In this study, we used a targeted SNP panel to construct a pedigree used for parentage analysis. Previous studies in the same sampling location identified patterns of local adaptation and sex-specific fitness effects using microsatellite markers in conjunction with parentage analysis (Mobley et al., 2019, 2020). The previous studies were conducted over four cohort years with only the largest class of potential offspring (0+) sampled within each cohort year separately. The advantage to using a targeted SNP panel was that it allowed sex typing and *vgll3* genotyping as well as provided neutral markers for parentage. Additionally, all year classes of juveniles and adults were incorporated into the multigenerational pedigree presented here. As a result, a higher proportion of offspring were assigned to parents when using all information. It is important to note that we used three different criteria for parentage assignment and our results were sensitive to priors used to construct the pedigree. For example, the three methods used in parentage assignment gave identical results with respect to offspring assigned to sampled females and nearly identical results to sampled males. However, these methods differed dramatically in the number of juvenile parr assigned as parents. One potential source of discrepancy between these methods may be that parentage analysis is assigning related individuals (parents and siblings) rather than true parents. Because this study samples in an open population of migrating individuals, it is near impossible to verify these relationships. However, refinement of priors to eliminate the most improbable relationships with the conservative data set led to the most biologically realistic interpretations of parentage.

Understanding the link between life history traits, reproductive fitness and the genetic underpinnings of such relationships is a fundamental goal of evolutionary biology. This study reveals sex-specific selection on a gene responsible for an important life-history trait. Balancing selection on females through overdominance contributes to the maintenance of polymorphism at the *vgll3* locus. Future studies that can investigate selection on adults in the marine environment may help to clarify internal and external sources for selection on this important life history gene. This study also demonstrates the utility of multigenerational pedigrees in investigating how sex-specific selection influences reproductive fitness and how genetic variation is maintained in natural populations.

AUTHOR CONTRIBUTIONS

C.R.P, J.E. and P.O. conceived the original idea; K.B.M., C.R.P. and H.J.B. conceived the study. M.E., K.B.M., P.O., O.G., H.P., and J.E. coordinated and/or participated in sample collection. C.R.P., A.R., and K.B.M. coordinated molecular data generation. H.J.B. performed parentage analysis. K.B.M. analysed the data. K.B.M. drafted the manuscript, with input from all other authors.

ACKNOWLEDGEMENTS

We thank Seija Tillanen, Katja Salminen, Meri Lindqvist, Jenni Kuismin, Jani Aaltonen, Susanna Ukonaho, Jan Laine, Oliver Andersson, Oona Mehtälä, Mikael Kyriacou and Shadi Jansouz for laboratory assistance and Tutku Aykanat for SNP panel assistance. Jorma Kuusela, Jari Haantie, and Matti Kylmäaho are thanked for scale aging analyses, and Topi Pöyhönen, Timo Kanniainen, Arto Koskinen, Jorma Ollila, Mari Lajunen, Tuomo Karjalainen (deceased), Mikko Kytökorpi, Seda Karslioglu, Anna Ellmen and Jukka-Pekka Verta for field assistance. We also thank two anonymous reviewers for helpful comments. Fishing permission for research purposes was granted by the Lapland Centre for Economic Development, Transport and the Environment (permit numbers 1579/5713-2007, 2370/5713-2012 and 1471/5713-2017) and approved annually by the local fishing management cooperative.

FUNDING INFORMATION

Funding (to C.R.P.) was provided by Academy of Finland (grant numbers 307593, 302873, 327255 and 342851), the University of Helsinki, and the European Research Council under the European Articles Union's Horizon 2020 and Horizon Europe research and innovation programs (grant nos. 742312 and 101054307). Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Neither the European Union nor the granting authority can be held responsible for them.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at [https://osf.io/tekvh/].

DATA AVAILABILITY STATEMENT

All data and code are available for download in the following repositories: [dataset] Barton HJ, Mobley KB; 2023; salmon_parentage:

release_for_publication; Zenodo; DOI: 10.5281/zenodo.10154280. [dataset] Mobley KB; 2023; Teno_salmon_pedigree; Zenodo; DOI: 10.5281/zenodo.10136609

BENEFITS GENERATED

We consulted with the indigenous and non-indigenous local fishing community and hired local community members, several of whom are included as co-authors, to help with sampling and develop sampling methodologies. Benefits from this research accrue from new knowledge promoting food and livelihood security and the sharing of our data and results on public databases as described above.

ORCID

Kenyon B. Mobley https://orcid.org/0000-0003-2843-6407
Craig R. Primmer https://orcid.org/0000-0002-3687-8435

REFERENCES

Ahi, E. P., Sinclair-Waters, M., Moustakas-Verho, J., Jansouz, S., & Primmer, C. R. (2022). Strong regulatory effects of vgll3 genotype on reproductive axis gene expression in juvenile male Atlantic salmon. *General and Comparative Endocrinology*, *325*, 114055.

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Åsheim, E. R., Debes, P. V., House, A., Liljeström, P., Niemelä, P. T., Siren, J. P., Erkinaro, J., & Primmer, C. R. (2023). Atlantic salmon (*Salmo salar*) age at maturity is strongly affected by temperature, population and age-at-maturity genotype. *Conservation Physiology*, *11*, coac086.

Aykanat, T., Johnston, S. E., Orell, P., Niemelä, E., Erkinaro, J., & Primmer, C. R. (2015). Low but significant genetic differentiation underlies biologically meaningful phenotypic divergence in a large Atlantic salmon population. *Molecular Ecology*, *24*, 5158–5174.

Aykanat, T., Lindqvist, M., Pritchard, V. L., & Primmer, C. R. (2016). From population genomics to conservation and management: A workflow for targeted analysis of markers identified using genome-wide approaches in Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *89*, 2658–2679.

Aykanat, T., Ozerov, M., Vähä, J.-P., Orell, P., Niemelä, E., Erkinaro, J., & Primmer, C. R. (2019). Co-inheritance of sea age at maturity and iteroparity in the Atlantic salmon *vgll3* genomic region. *Journal of Evolutionary Biology*, *32*, 343–355.

Aykanat, T., Rasmussen, M., Ozerov, M., Niemelä, E., Paulin, L., Vähä, J. P., Hindar, K., Wennevik, V., Pedersen, T., Svenning, M. A., & Primmer, C. R. (2020). Life history genomic regions explain differences in Atlantic salmon marine diet specialization. *Journal of Animal Ecology*, *89*, 2677–2691.

Bangura, P. B., Tiira, K., Niemelä, P. T., Erkinaro, J., Liljeström, P., Toikkanen, A., & Primmer, C. R. (2022). Linking vgll3 genotype and aggressive behaviour in juvenile Atlantic salmon (Salmo salar). *Journal of Fish Biology*, *100*, 1264–1271.

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., Jacq, C., Jensen, A. J., Johnston, S. E., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Næsje, T. F., Orell, P., Romakkaniemi, A., Sægrov, H., Urdal, K., … Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, *528*, 405–408.

Birnie-Gauvin, K., Bordeleau, X., Eldøy, S. H., Bøe, K., Kristensen, M. L., Nilsen, C. I., & Lennox, R. J. (2023). A review of iteroparity in anadromous salmonids: Biology, threats and implications. *Reviews in Fish Biology and Fisheries*, *33*, 1005–1025.

Bordeleau, X., Pardo, S. A., Chaput, G., April, J., Dempson, B., Robertson, M., Levy, A., Jones, R., Hutchings, J. A., Whoriskey, F. G., & Crossin, G. T. (2020). Spatio-temporal trends in the importance of iteroparity across Atlantic salmon populations of the northwest Atlantic. *ICES Journal of Marine Science*, *77*, 326–344.

Brown, K. E., & Kelly, J. K. (2018). Antagonistic pleiotropy can maintain fitness variation in annual plants. *Journal of Evolutionary Biology*, *31*, 46–56.

Christie, M. R., McNickle, G. G., French, R. A., & Blouin, M. S. (2018). Life history variation is maintained by fitness trade-offs and negative frequency-dependent selection. *Proceedings of the National Academy of Sciences*, *115*, 4441–4446.

Connallon, T., & Clark, A. G. (2014). Balancing selection in species with separate sexes: Insights from Fisher's geometric model. *Genetics*, *197*, 991–1006.

Connallon, T., Cox, R. M., & Calsbeek, R. (2010). Fitness consequences of sex-specific selection. *Evolution*, *64*, 1671–1682.

Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., & Primmer, C. R. (2018). Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. *Nature Ecology & Evolution*, *2*, 1800–1807.

Debes, P. V., Piavchenko, N., Ruokolainen, A., Ovaskainen, O., Moustakas-Verho, J. E., Parre, N., Aykanat, T., Erkinaro, J., & Primmer, C. R. (2021). Polygenic and major-locus contributions to sexual maturation timing in Atlantic salmon. *Molecular Ecology*, *30*, 4505–4519.

Einum, S., Thorstad, E. B., & Næsje, T. F. (2002). Growth rate correlations across life-stages in female *Atlantic salmon*. *Journal of Fish Biology*, *60*, 780–784.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science*, *197*, 215–223.

Erkinaro, J., Czorlich, Y., Orell, P., Kuusela, J., Falkegård, M., Länsman, M., Pulkkinen, H., Primmer, C. R., & Niemelä, E. (2019). Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*, 42–55.

Erkinaro, J., Dempson, J. B., Julkunen, M., & Niemelä, E. (1997). Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: An approach based on analysis of scale characteristics. *Journal of Fish Biology*, *51*, 1174–1185.

Erkinaro, J., & Niemelä, E. (1995). Growth differences between the Atlantic salmon parr,Salmo salar, of nursery brooks and natal rivers in the river Teno watercourse in northern Finland. *Environmental Biology of Fishes*, *42*, 277–287.

Erkinaro, J., Niemelä, E., Saari, A., Shustov, Y., & Jørgensen, L. (1998). Timing of habitat shift by Atlantic salmon parr from fluvial to lacustrine habitat: Analysis of age distribution, growth, and scale characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2266–2273.

Fleming, I. (1998). Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 59–76.

Fleming, I., & Reynolds, J. D. (2004). Salmonid breeding systems. In *Evolution illuminated: Salmon and Their relatives* (p. 264). Hendry AP.

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*, 379–416.

Fleming, I. A., & Einum, S. (2011). Reproductive ecology: A tale of two sexes. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic salmon ecology* (pp. 33–65). Wiley-Blackwell.

Halperin, D. S., Pan, C., Lusis, A. J., & Tontonoz, P. (2013). Vestigial-like 3 is an inhibitor of adipocyte differentiation. *Journal of Lipid Research*, *54*, 473–481.

Hard, J. J., Gross, M. R., Heino, M., Hilborn, R., Kope, R. G., Law, R., & Reynolds, J. D. (2008). SYNTHESIS: Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications*, *1*, 388–408.

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models.

Harvey, A., Skaala, Ø., Borgstrøm, R., Fjeldheim, P. T., Christine Andersen, K., Rong Utne, K., Askeland Johnsen, I., Fiske, P., Winterthun, S., Knutar, S., Sægrov, H., Urdal, K., & Alan Glover, K. (2022). Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecology and Evolution*, *12*, e8780.

Heinimaa, S., & Erkinaro, J. (2004). Characteristics of mature male parr in the northernmost Atlantic salmon populations. *Journal of Fish Biology*, *64*, 219–226.

House, A. H., Debes, P. V., Kurko, J., Erkinaro, J., & Primmer, C. R. (2023). Genotype-specific variation in seasonal body condition at a large-effect maturation locus. *Proceedings of the Royal Society B: Biological Sciences*, *290*, 20230432.

Huisman, J. (2017). Pedigree reconstruction from SNP data: Parentage assignment, sibship clustering and beyond. *Molecular Ecology Resources*, *17*, 1009–1024.

Hutchings, J. A., & Myers, R. A. (1988). Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. *Oecologia*, *75*, 169–174.

Hutchings, J. A., & Myers, R. A. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, *8*, 256–268.

Johnston, S. E., Gratten, J., Berenos, C., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Slate, J. (2013). Life history trade-offs at a single locus maintain sexually selected genetic variation. *Nature*, *502*, 93–95.

Jones, M. W., & Hutchings, J. A. (2002). Individual variation in Atlantic salmon fertilization success: Implications for effective population size. *Ecological Applications*, *12*, 184–193.

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown trout: Habitat as a template for life histories*. Springer.

Kuparinen, A., & Hutchings, J. A. (2019). When phenotypes fail to illuminate underlying genetic processes in fish and fisheries science. *ICES Journal of Marine Science*, *76*, 999–1006.

Mank, J. E. (2017). Population genetics of sexual conflict in the genomic era. *Nature Reviews Genetics*, *18*, 721–730.

Mérot, C., Llaurens, V., Normandeau, E., Bernatchez, L., & Wellenreuther, M. (2020). Balancing selection via life-history trade-offs maintains an inversion polymorphism in a seaweed fly. *Nature Communications*, *11*, 670.

Mobley, K. B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J. P., & Primmer, C. R. (2021). Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): A synthesis of ecological, genetic, and molecular processes. *Reviews in Fish Biology and Fisheries*, *31*, 523–571.

Mobley, K. B., Granroth-Wilding, H., Ellmen, M., Vähä, J. P., Aykanat, T., Johnston, S. E., Orell, P., Erkinaro, J., & Primmer, C. R. (2019). Home ground advantage: Local Atlantic salmon have higher reproductive fitness than dispersers in the wild. *Science Advances*, *5*, eaav1112.

Mobley, K. B., Granroth-Wilding, H., Ellmen, M., et al. (2020). Time spent in distinct life-history stages has sex-specific effects on reproductive fitness in wild Atlantic salmon. *Molecular Ecology*, *29*, 1173–1184.

Niemelä, P. T., Klemme, I., Karvonen, A., Hyvärinen, P., Debes, P. V., Erkinaro, J., Sinclair-Waters, M., Pritchard, V. L., Härkönen, L. S., & Primmer, C. R. (2022). Life-history genotype explains variation in migration activity in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20220851.

Økland, F., Jonsson, B., Jensen, A. J., & Hansen, L. P. (1993). Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? *Journal of Fish Biology*, *42*, 541–550.

Persson, L., Raunsgard, A., Thorstad, E. B., Østborg, G., Urdal, K., Sægrov, H., Ugedal, O., Hindar, K., Karlsson, S., Fiske, P., & Bolstad, G. H. (2023). Iteroparity and its contribution to life-history variation in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*, 577–592.

Prokkola, J. M., Åsheim, E. R., Morozov, S., Bangura, P., Erkinaro, J., Ruokolainen, A., Primmer, C. R., & Aykanat, T. (2022). Genetic coupling of life-history and aerobic performance in Atlantic salmon. *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20212500.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Seamons, T. R., & Quinn, T. P. (2010). Sex-specific patterns of lifetime reproductive success in single and repeat breeding steelhead trout (*Oncorhynchus mykiss*). *Behavioral Ecology and Sociobiology*, *64*, 505–513.

Sinclair-Waters, M., Ødegård, J., Korsvoll, S. A., Moen, T., Lien, S., Primmer, C. R., & Barson, N. J. (2020). Beyond large-effect loci: Large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. *Genetics Selection Evolution*, *52*, 9.

Sinclair-Waters, M., Piavchenko, N., Ruokolainen, A., Aykanat, T., Erkinaro, J., & Primmer, C. R. (2022). Refining the genomic location of single nucleotide polymorphism variation affecting Atlantic salmon maturation timing at a key large-effect locus. *Molecular Ecology*, *31*, 562–570.

Thorpe, J. E. (2007). Maturation responses of salmonids to changing developmental opportunities. *Marine Ecology Progress Series*, *335*, 285–288.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. Springer.

Verta, J.-P., Debes, P. V., Piavchenko, N., Ruokolainen, A., Ovaskainen, O., Moustakas-Verho, J. E., Tillanen, S., Parre, N., Aykanat, T., Erkinaro, J., & Primmer, C. R. (2020). Cis-regulatory differences in isoform expression associate with life history strategy varation in Atlantic salmon. *PLoS Genetics*, *16*, e1009055.

Warnes, G. (2012). *Genetics*.

Wright, A. E., Fumagalli, M., Cooney, C. R., Bloch, N. I., Vieira, F. G., Buechel, S. D., Kolm, N., & Mank, J. E. (2018). Male-biased gene expression resolves sexual conflict through the evolution of sex-specific genetic architecture. *Evolution Letters*, *2*, 52–61.

Xiang, T., Christensen, O. F., Vitezica, Z. G., & Legarra, A. (2018). Genomic model with correlation between additive and dominance effects. *Genetics*, *209*, 711–723.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mobley, K. B., Barton, H. J., Ellmén, M., Ruokolainen, A., Guttorm, O., Pieski, H., Orell, P., Erkinaro, J., & Primmer, C. R. (2024). Sex-specific overdominance at the maturation *vgll3* gene for reproductive fitness in wild Atlantic salmon. *Molecular Ecology*, *33*, e17435. https://doi.org/10.1111/mec.17435