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Variation in phenotypic plasticity across age-at-maturity genotypes in wild Atlantic salmon

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Abstract

Evolution of phenotypic plasticity requires genotype–environment interaction. The discovery of two large-effect loci in the *vgll3* and *six6* genomic regions associated with the number of years the Atlantic salmon spend feeding at sea before maturation (sea age), provides a unique opportunity to study evolutionary potential of phenotypic plasticity. Using data on 1246 Atlantic salmon caught in the River Surna in Norway, we show that variation in mean sea age among years (smolt cohorts 2013–2018) is influenced by genotype frequencies as well as interaction effects between genotype and year. Genotype–year interactions suggest that genotypes may differ in their response to environmental variation across years, implying genetic variation in phenotypic plasticity. Our results also imply that plasticity in sea age will evolve as an indirect response to selection on mean sea age due to a shared genetic basis. Furthermore, we demonstrate differences between years in the additive and dominance functional genetic effects of *vgll3* and *six6* on sea age, suggesting that evolutionary responses will vary across environments. Considering the importance of age at maturity for survival and reproduction, genotype–environment interactions likely play an important role in local adaptation and population demography in Atlantic salmon.

KEYWORDS
age at maturity, Atlantic salmon, genetic variation, phenotypic plasticity

1 | INTRODUCTION

Phenotypic plasticity, defined as the ability of a genotype to produce different phenotypes in different environments, can evolve as an adaptation to variable environments (Bradshaw, 1965; Ghalambor et al., 2007). Understanding phenotypic plasticity in fitness-related traits is fundamental for predicting how populations will cope with environmental changes in nature (Chevin & Lande, 2010; Kelly, 2019; Reid & Acker, 2022). Plasticity may evolve if there is genetic variation within a population in how individuals respond across environments (genotype by environment interaction) and if the traits involved affect fitness (Scheiner, 1993; Via & Lande, 1985).

Genetic variation in plasticity has mainly been demonstrated in experimental studies (Hutchings et al., 2007; Newman, 1994; Oomen & Hutchings, 2015; Stinchcombe et al., 2004). Studies in wild populations have demonstrated variation among individuals in plasticity in traits that are expressed repeatedly during an individual's lifetime (Hendry, 2015), for example in breeding date in long-lived

birds (Brommer et al., 2005; Nussey, Postma, et al., 2005) or mammals (Nussey, Clutton-Brock, et al., 2005). Recent discoveries of loci or genomic regions explaining large proportions of the variation in life-history traits (e.g. age at maturity: Barson et al., 2015; reproductive strategies: Lamichhaney et al., 2016; maturation traits: Narum et al., 2018), open new opportunities to study genetic variation in plasticity in wild populations also in traits that are expressed only once during an individual's lifetime.

Age at maturity is a key life-history trait that impacts fitness and population demography through effects on fecundity, survival and generation time (Cole, 1954). Atlantic salmon (*Salmo salar*) spend 1–5 years feeding at sea, often referred to as sea age, before they return for reproduction to the river where they hatched and grew up as juveniles, or a nearby river (Fleming, 1996). Like in many other species, age at maturity in Atlantic salmon represents an evolutionary trade-off: later-maturing and larger individuals achieve greater reproductive success, but at an increased risk of dying before the first reproduction (Fleming, 1998). Female Atlantic salmon have a direct reproductive advantage of late maturation due to the strong positive correlations between age and body size, and body size and egg production (O'Sullivan et al., 2019). Males do not have the direct effect of higher fecundity with larger body size, but a larger body size is important in male–male competition and sexual selection (Fleming, 1996). Because males can use the alternative tactic to access females as sneakers, selection for a large body size is weaker in males than in females (Fleming & Einum, 2011), which is reflected in the sexual dimorphism in size and age at maturity (Barson et al., 2015).

Sea age at maturity is a highly heritable trait; heritability of maturing after 1 year at sea ranges from 0.51 to 0.84 on the liability scale (Reed et al., 2019; Sinclair-Waters et al., 2020) and from 0.48 to 0.61 on the observed scale (Gjerde, 1984; Sinclair-Waters et al., 2020). Previous work suggests that sea age is influenced by a combination of large-effect and smaller-effect loci (Sinclair-Waters et al., 2020, 2022). Two loci likely play a key role, one in the *vgll3* genomic region on chromosome 25 and one in the *six6* genomic region on chromosome nine. Of these, *vgll3* has the strongest and most consistent effect across studies, explaining 19%–39% of the variation in sea age (Ayllon et al., 2015; Barson et al., 2015; Sinclair-Waters et al., 2022), while *six6* has been found to explain up to 9% of the variation in sea age (Sinclair-Waters et al., 2022). Sea age at maturity is also presumed to be strongly influenced by environmental conditions, particularly during the marine phase (Mobley et al., 2021).

We used data on individual Atlantic salmon collected during an eight-year period in the Norwegian River Surna to study phenotypic plasticity in age at maturity for different genotypes of the large-effect loci in the *vgll3* and *six6* genomic regions. Scales collected from adult fish when they had returned to the river for spawning were used for age determination and genetic analyses. First, we quantified how much of the among-year variation in sea age could be explained by changes in genotype frequencies of *vgll3* and *six6*. Second, we included a genotype–year interaction in the model, where each year represents a unique environment, to quantify differences in plasticity (among-year variation in sea age) among genotypes. Third, we estimated variation among years in the sex-specific additive and dominance effects of *vgll3* and *six6* on sea age.

2 | MATERIALS AND METHODS

2.1 | Study population

Surna is a medium-sized river located in mid-Norway (62°58′25″ N, 8°38′54″ E), with an estimated yearly run of Atlantic salmon of 2300–3900 individuals in 2014–2021 (Table S1). Salmon are harvested in a recreational rod-fishery which takes place from June 1st to August 31st each year. Anglers provide scale samples of harvested fish with information on place and date of capture, fish length, weight, presence/absence of the adipose fin and sex. We received samples from 45% to 65% of the harvested salmon in 2014–2021. These samples covered most of the run-time in Surna, and we therefore consider our data as largely representative of the population (cf. Harvey et al., 2017). However, the data are skewed towards males. This may partly be explained by: (1) males spend, on average, a shorter time at sea than females, which increases the probability of surviving the marine migration and returning to the river; (2) error in sex determination may skew the sex ratio towards males, because the most common error made by anglers is to mistake females for males (King et al., 2023; Robertsen et al., 2021); Finally, (3) females (>70 cm) are protected in the last part of the fishing season, which may add to the skewed sex ratio. However, there are very few large females returning to the river late in the season. Because of the skewed sex ratio, we have analysed the sexes separately. To compensate for reduced natural production of juveniles due to hydropower development in 1968, Surna is annually stocked with salmon smolts (about 35,000) and parr (about 60,000).

2.2 | Phenotypic traits and genetic analyses

By analysing scales, we recorded the number of years individual salmon had spent in the river before migrating to sea as smolts, the number of years spent at sea before returning to the river to spawn (sea age), whether the salmon had spawned before, and whether the salmon was wild or an escapee from a salmon farm (Lund & Hansen, 1991). From sampling year and sea age, each fish was assigned a year of outmigration to sea as smolt. Fish of stocked origin were identified by a removed adipose fin and genetic methods (parent–offspring analyses; Hagen et al., 2021). Escaped farmed salmon were identified based on the scale-growth pattern. Escaped farmed salmon and hatchery-produced salmon were excluded from all analyses. The total sample of aged wild salmon was 2534 individuals (Table S1). A subset of 1234 individuals (430 females and 804 males) were assayed for genetic variation in the $vgll3_{TOP}$ and $six6_{TOP}$ loci, which are the single-nucleotide polymorphisms (SNPs) most highly associated with variation in sea age in Barson et al. (2015); Tables S2

and S3). In the rest of the paper, we refer to these loci as *vgll3* and *six6*, which are the names of the candidate genes in the proximity of the two SNPs. DNA was extracted from scale samples using DNEASY tissue kit (QIAGEN) and genotyped on the EP1™ 96.96 Dynamic array IFCs platform (Fluidigm).

2.3 | Statistical analyses

2.3.1 | Correcting for variation in sampling intensity

Individuals that migrate to sea as smolts the same year (smolt cohort) likely experience similar environmental conditions during the first weeks or months at sea, and the conditions they experience during this phase may influence how many years they spend at sea before they return to spawn (Mobley et al., 2021; Tréhin et al., 2023). The most relevant level of analysis is therefore at the smolt-cohort level, but because our data are based on fish that were sampled when they returned to the river, variation among sample years in the number of returning salmon, as well as sampling intensity, will influence the observed mean sea age of a given smolt cohort. Our estimates of mean sea age within smolt cohorts were corrected for variation among sampling years by combining the observed sea age distribution in the scale data set ($n = 2534$) and estimates of the total number of returning salmon in a given sample year (Table S1). Estimates of yearly returns were obtained from the Norwegian Scientific Advisory Committee for Atlantic Salmon Management, and are based on catch data and exploitation rates (Forseth et al., 2013). The estimates of yearly returns also include hatchery-produced salmon, and because these were not included in our analyses, we adjusted down the number of returns in each year with the annual proportions of hatchery-produced fish in the scale data set.

We calculated the number of wild salmon in each age group returning in sample year t as

$$N_i(t) = \frac{n_i(t)}{n_{tot}(t)} N_{ret}(t)\left(1 - P_{hatch}(t)\right),$$

where for each capture year t, n_i is the number of aged fish of sea age i and n_{tot} is the total number of aged fish, N_{ret} is the estimated number of returning fish, and P_{hatch} is the proportion of hatchery-produced fish. Mean sea age at first reproduction corrected for sampling variation, $\overline{X}(T)$, for the smolt cohort migrating to sea in year T, is given by

$$\overline{X}(T) = \sum_{i=1}^{7} i \frac{N_i(T+i)}{N_{SC}(T)},$$

where $N_{sc}(T) = \sum_{i=1}^{7} N_i(T+i)$ is the total number of surviving fish in the smolt cohort migrating to sea in year T, and hence, the ratio in the equation gives the proportion of fish of each sea age from 1 to 7, i, of the smolt cohort. The difference between the mean sea age in the data sets used in the analyses and the mean sea age corrected for sampling intensity was included as an offset variable in all models that included individual sea age as a response variable, to remove the effect of sampling variation on sea age. This is equivalent to directly using adjusted individual sea ages as response variables in these models.

2.3.2 | Error correction of variances

Part of the variance in a set of estimates (e.g. yearly means) is due to error in the estimates. To assess whether the variance in annual mean sea age and annual genetic effects exceeded the estimation variance, we calculated the error-corrected variance as

$$\sigma_\beta^2 = \mathrm{Var}(\beta) - \overline{SE_\beta^2},$$

where $\mathrm{Var}(\beta)$ is the observed among-year variance in the focal variable β and $\overline{SE_\beta^2}$ is the average squared standard error of the annual estimates. The among-year error-corrected standard deviation of β is given by σ_β.

2.3.3 | Genetic contribution of *vgll3* and *six6* to among-year variation in sea age

Differences between smolt cohorts in mean sea age may reflect environmental variation, genetic variation, or a combination of both. To assess the combined contribution of genetic effects of *vgll3* and *six6* to variation in sea age among smolt cohorts, we compared estimates of annual mean sea age from models including versus excluding genetic effects of *vgll3* and *six6*. For each sex, we fitted a linear least-squares model with individual sea age at first reproduction as the response variable and smolt cohort (2013–2018) and genetic effects of *vgll3* and *six6* as predictor variables. Note that the method of least squares does not assume normally (Gaussian) distributed residuals for estimating the regression parameters and their associated standard errors. Previous studies have shown that the two *vgll3* alleles are associated with either early (E) or late (L) maturation and that there is a near complete additive effect in females (i.e. linear effect of number of L alleles on sea age in females) and dominance for the E allele in males (i.e. the EL genotype is more similar to the EE genotype in terms of sea age; Barson et al., 2015). We therefore split effects of *vgll3* into its functional additive and dominance component (Álvarez-Castro & Carlborg, 2007). Additive effects of *vgll3* were coded as number of late (L) alleles (0, 1 or 2) and dominance effects as 1 for heterozygote individuals (one E and one L allele) and 0 for homozygote individuals (two E or two L alleles). Effects of *six6* were coded in the same way. We label these effects 'functional' as their estimates do not depend on the genotype frequencies at the locus, in contrast to 'statistical' genetic effects (Álvarez-Castro & Carlborg, 2007; Cheverud & Routman, 1995; Hansen & Wagner, 2001). Due to low frequency of the *six6* E allele, the EE genotype was rare and was not observed in females in the 2015 samples. For this reason, we could not estimate the additive and the dominance effect of *six6*

for females in 2015, and the dominance effect was set to 0. We compared the variance in estimated annual mean sea age from this model to the variance in estimated annual mean sea age from a model excluding effects of *vgll3* and *six6*. The latter among-year variance will include variance due to genotype frequency variation, while the former will not. If genotype frequencies are constant across years, the two models will yield similar estimates of the among-year variance. The difference between the two models in the estimated among-year variance can therefore be interpreted as the part of the variance among smolt cohorts that is due to variation in *vgll3* and *six6* genotype frequency (see Figures S1 and S2 for variation in allele frequencies and genotype frequencies over smolt cohorts and return cohorts).

The freshwater environment may also influence sea age (e.g. Salminen, 1997). Thus, variation in sea age among smolt cohorts may be due to variation among smolt cohorts in number of years spent in freshwater (smolt age). Using the subset of the data that included information on smolt age ($n = 1100$), we fitted the models above with smolt age included as a covariate, to examine if variation in smolt age contributed to the variation in sea age among smolt cohorts (see Figure S3).

2.3.4 | Genotype–year interaction effects on sea age

If individuals migrating to the sea in the same year experience similar environmental conditions, differences between genotypes in how sea age varies among smolt cohorts would indicate differences between genotypes in their plastic response to environmental conditions (genotype–environment interaction). To assess whether there were differences between *vgll3* genotypes or between *six6* genotypes in plasticity, we fitted a linear least-squares model for each sex, with sea age as the response variable and additive and dominance effects of *vgll3* and *six6*, and their interactions with smolt cohort as predictor variables. We compared the variance among smolt cohorts and genotypes in mean sea age from this model to the variance in mean sea age from a model excluding the interactions between smolt cohort and genotype. The difference in variance can be interpreted as the part of the variance among smolt cohorts and genotypes that is due to a genotype-by-smolt cohort interaction. For the subset including data on smolt age, we examined whether including smolt age as a covariate influenced the results (Figures S4 and S5).

2.3.5 | Evolvability

Evolvability can be measured as the mean-standardized additive genetic variance (Hansen et al., 2003, 2011; see also Houle, 1992). This evolvability measure can be interpreted as proportional increase in the trait mean under unit strength selection (i.e. selection gradient = 1), which is strong selection as it equals the strength of selection on fitness itself (Hansen et al., 2003). We used the estimated genetic effects of *vgll3* and *six6* to calculate single-locus evolvabilities. For each sex, single-locus evolvability of locus i is given by

$$e_i = \frac{V_{Ai}}{\bar{z}^2}$$

where $\bar{z}$ is the sex-specific mean sea age and V_{Ai} is the sex-specific additive genetic variance at locus i. The additive genetic variance of locus i is given by

$$V_{Ai} = 2p_i(1-p_i)\left(a_i + d_i(1-2p_i)\right)^2 - Bias$$

$$Bias = 2p_i(1-p_i)\left(\mathrm{Var}[a_i] + (1-2p_i)^2\mathrm{Var}[d_i] + 2(1-2p_i)\mathrm{Cov}[a_i d_i]\right)$$

where p_i is the locus' allele frequency, a_i and d_i are its sex-specific additive and dominance effects, and $Var[a_i]$, $Var[d_i]$ and $Cov[a_i d_i]$ are the error variances and error covariance for the additive and dominance effects (Monnahan & Kelly, 2015). We used the same method to estimate smolt-cohort-specific single-locus evolvabilities, by using the estimated annual genetic effects and the sex-specific mean sea age of each smolt cohort.

To calculate the error-corrected among-year standard deviation in single-locus evolvability, we first sampled from 1000 values of a and d from their error-corrected among-year variance matrix (Table S4), assuming a bivariate normal distribution. We constrained this matrix to have positive variances and correlations within the range −1 to 1. For each of these samples, we calculated the V_{Ai} according to the above equation (with $Bias = 0$), using the global average allele frequency for each locus. From this distribution, we calculated the error-corrected among-year standard deviation in evolvability as $\sigma_{ei} = \mathrm{SD}[V_{Ai}] / \bar{z}$, where $\mathrm{SD}[V_{Ai}]$ is the standard deviation of the sampled V_{Ai} values and $\bar{z}$ is the sex-specific mean sea age.

Total evolvability, which includes the effects of all loci influencing sea age, can be estimated by $e = V_P h^2 / \bar{z}^2$, where V_P is the phenotypic variance of sea age and h^2 is the heritability of sea age. We compared single-locus evolvabilities to two different estimates of total evolvability: assuming $h^2 = 0.5$ or $h^2 = 1$ (i.e. half or all of the phenotypic variance is explained by the additive genetic variance). In the results, evolvabilities are given in percentages (i.e. $e \times 100$).

2.3.6 | Statistical software

All analyses were done using Rstudio running R v.4.3.1 (R Core Team, 2023). Packages broom (Robinson et al., 2023), dplyr (Wickham et al., 2023), stringr (Wickham, 2022) and tidyr (Wickham & Girlich, 2023) were used for data wrangling tasks. The ggeffects package (Lüdecke, 2018) was used for generating model predictions. Figures were produced using the packages ggplot2 (Wickham, 2016) and patchwork (Pedersen, 2023), and tables were produced using the package flextable (Gohel & Skintzos, 2023).

3 | RESULTS

3.1 | Genetic contribution of *vgll3* and *six6* to among-year variation in sea age

Mean sea age at first reproduction varied among smolt cohorts in both females and males, ranging from 2.03 to 2.41 years in females and from 1.55 to 1.98 years in males (Figure 1a; Table S5). Mean sea age in the different years was positively correlated between females and males (Figure 1a; correlation: 0.84).

In females, the effect of *vgll3* on sea age was completely additive, with sea age increasing by 0.22 ± 0.04 years per L allele (dominance effect: −0.02 ± 0.06), resulting in LL females being on average 0.45 years older than EE females (Figure 1b; Table S6). In males, sea age increased by 0.38 ± 0.04 years per L allele, but there was almost complete dominance for the E allele (dominance effect of −0.36 ± 0.05; Figure 1b; Table S6). Hence, LL males were on average 0.76 years older than EE males, and 0.74 years older than EL males. The effect of *six6* on sea age was generally weaker than the effect of *vgll3* in both sexes (Figure 1c; Table S6). For each *six6* L allele added, sea age increased by 0.12 ± 0.05 years in females and 0.09 ± 0.04 years in males. Dominance effects were −0.10 ± 0.06 for females and 0.04 ± 0.06 for males (Figure 1c; Table S6).

Variation among smolt cohorts in mean sea age was partly explained by variation in the *vgll3* and *six6* genotype frequency. This is illustrated in Figure 1a by the difference in the predicted annual mean sea age from the models controlling for effects of *vgll3* and *six6* (dashed line) versus the models not controlling for effects of *vgll3* and *six6* (solid lines). The variance in predicted mean sea age among smolt cohorts was 28% and 16% lower when controlling for effects of *vgll3* and *six6*, for females and males, respectively.

To evaluate the evolutionary importance of a locus in the population, we can calculate its evolvability from the genetic effects and the allele frequency. In females, the single-locus evolvabilities were 0.41% and 0.22% for *vgll3* and *six6*, respectively. In males, the corresponding numbers were 1.16% and 0.05%. Assuming a heritability of 0.5, the total evolvability of sea age in the Surna salmon population was estimated at 3.28% and 8.11% in females and males, respectively. In this case, the combined contribution of *vgll3* and *six6* to total evolvability was 19.3% in females and 14.8% in males. As an upper limit, we can assume that all the phenotypic variance is attributed to additive genetic variance (i.e. $h^2 = 1$). In this case, the combined contribution of *vgll3* and *six6* to total evolvability was 9.6% and 7.4% in females and males, respectively.

3.2 | Genotype–year interaction effects on sea age

The interaction between *vgll3* genotype and smolt cohort accounted for 46% (females) and 24% (males) of the observed variance in mean sea age among all combinations of genotypes and years (Table 1; Figure 2a). The corresponding numbers for *six6* were 58% for females

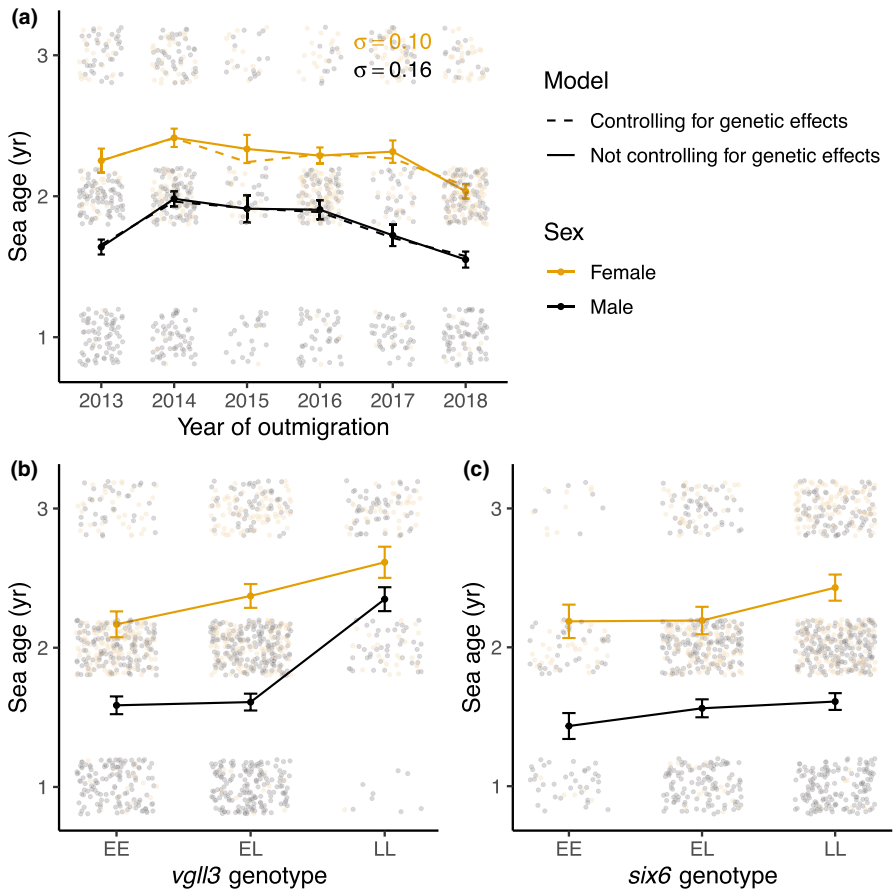

FIGURE 1 (a) Mean sea age of females and males returning to spawn from smolt cohorts 2013 to 2018 (solid lines). Error-corrected among-year standard deviations are denoted by σ. Dashed lines show the mean sea age after controlling for *vgll3* and *six6*. (b) Effect of *vgll3*, and (c) *six6* genotypes on sea age, where E represents the allele associated with early maturation, and L represents the allele associated with late maturation. Filled circles in the background indicate individual sea ages. Individuals with sea ages ≥3 are pooled in the plot. Vertical bars indicate ± one standard error.

and 36% for males (Table 1; Figure 3a), but the variance estimates for *six6* had high error components. These results suggest that there are differences among genotypes in how they respond to environmental variation across years.

Among the *vgll3* genotypes, the LL genotype had the largest variation in sea age among years, with an error-corrected standard deviation of 0.13 years in females and 0.25 years in males (Figure 2a). Among the *six6* genotypes, the EE genotype had the largest variation in sea age among years, with an error-corrected standard deviation of 0.24 years in females and 0.21 years in males (Figure 3a).

In females, the additive effect of *vgll3* ranged from 0.12 ± 0.09 years (in 2016) to 0.41 ± 0.21 years (in 2013), and the dominance effect ranged from −0.51 ± 0.22 years in 2015 to 0.12 ± 0.12 years in 2016 (Figure 2b; Table S7). All among-year variance in the additive effect of *vgll3* was explained by uncertainty in the estimates (observed variance of 0.01 and $\overline{SE^2}$ of 0.02), and there were no statistically significant differences between years (Table S8). There was, however, variation among years in the dominance effect of *vgll3*, with an error-corrected standard deviation of 0.13 years (62% of the variance was due to uncertainty), and two out of 15 pairwise differences between years in the dominance effect were statistically significant (Table S9). In most years, the mean sea age of the heterozygote (EL) genotype was intermediate of the EE and LL genotype, but in 2015 it was similar to the EE genotype, and in 2016 it was similar to the LL genotype (Figure 2a, green line).

In males, the general pattern across years was that the *vgll3* EE and EL genotype had similar mean sea age, while the LL genotype was older (Figure 2a). There was, however, variation among years both in the additive and dominance effect of *vgll3* (Figure 2b; Table S7). When accounting for uncertainty in the estimates, the standard deviation was 0.09 years in the additive effect and 0.19 years in the dominance effect (61% and 36% of the variance was due to uncertainty in the additive and dominance effect, respectively). Two out of 15 pairwise differences in the additive effect, and three out of 15 pairwise differences in the dominance effect, were statistically significant (Tables S10 and S11). In two years, the difference in mean sea age between the EE/EL and the LL genotype was particularly large. In 2015 and 2017, the LL genotype was 1.19 ± 0.31 and 1.00 ± 0.24 years older than the EE genotype, whereas 2016 was the year with the weakest effect of *vgll3*, when the LL genotype was only 0.41 ± 0.20 years older than

TABLE 1 Variance in sea age among all combinations of smolt cohorts (years) and genotypes, and the percentage of this variance explained by the genotype–year interaction (G × Y) and by error in the estimates. Error-corrected standard deviations (σ) are given for comparison.

Gene	Sex	Variance (yr^2)	G × Y	Error	σ (yr)
vgll3	Female	0.084	46%	35%	0.233
	Male	0.206	24%	9%	0.433
six6	Female	0.062	58%	41%	0.191
	Male	0.045	36%	50%	0.150

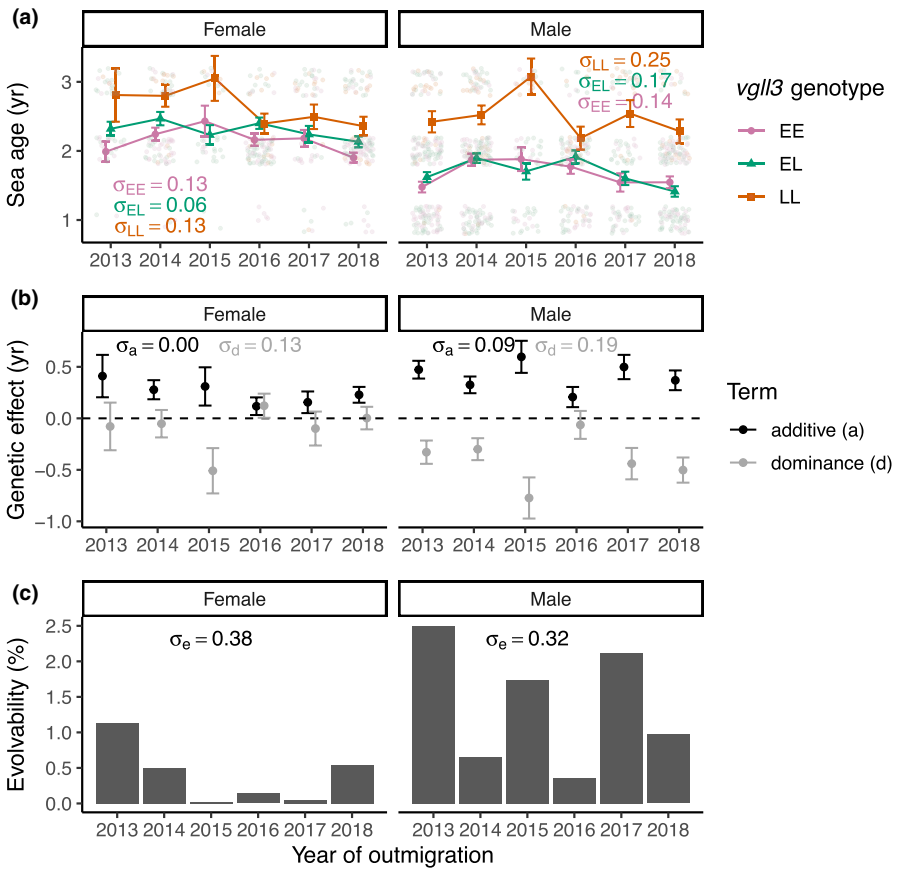

FIGURE 2 (a) Mean sea age (± one standard error) of females and males of different *vgll3* genotypes for the different smolt cohorts (year of outmigration from the river to the sea). Error-corrected among-year standard deviations are denoted by σ. Filled circles in the background indicate individual sea ages. Individuals with sea ages ≥3 are pooled in the plot. (b) Additive and dominance (functional) genetic effects of *vgll3* (± one standard error) for the different smolt cohorts, with error-corrected among-year standard deviations (σ). (c) The single-locus evolvability of *vgll3* in each smolt cohort, with error-corrected among-year standard deviations (σ).

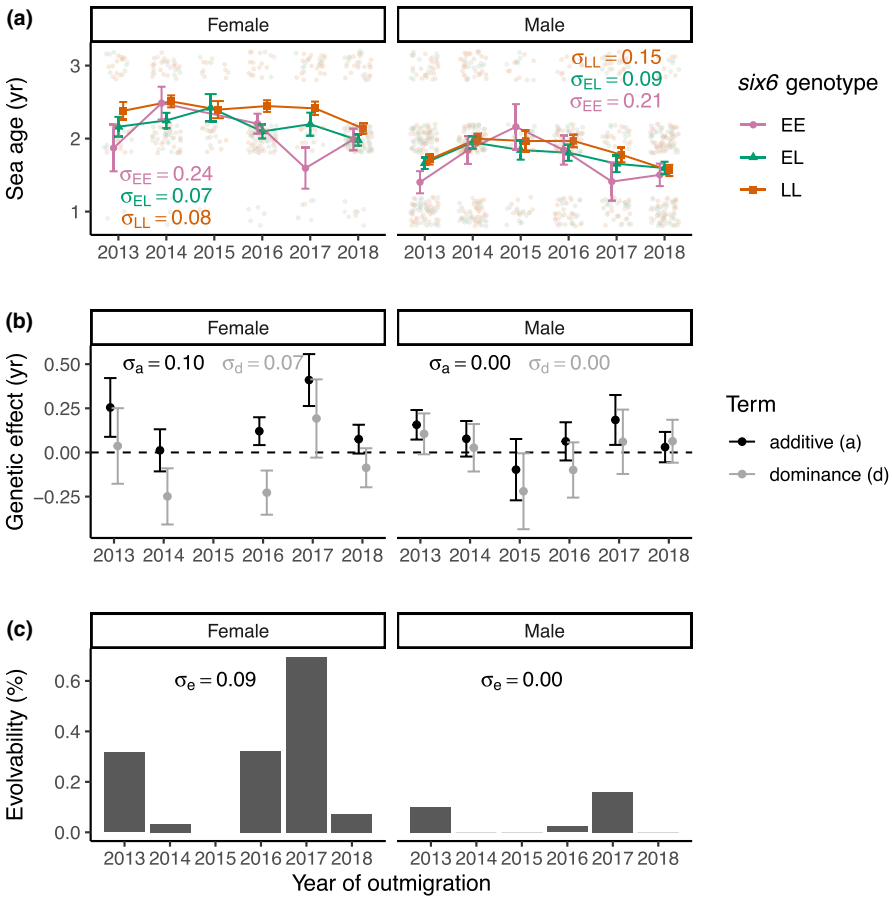

FIGURE 3 (a) Mean sea age (± one standard error) of females and males of different *six6* genotypes for the different smolt cohorts (year of outmigration from the river to the sea). Error-corrected among-year standard deviations are denoted by σ. Filled circles in the background indicate individual sea ages. Individuals with sea ages ≥3 are pooled in the plot. (b) Additive and dominance (functional) genetic effects of *six6* (± one standard error) for the different smolt cohorts, with error-corrected among-year standard deviations (σ). (c) The single-locus evolvability of *six6* in each smolt cohort, with error-corrected among-year standard deviations (σ).

the EE genotype. In 2016, there was no dominance and only a small additive effect (Figure 2b; Table S7).

In females, the additive effect of *six6* ranged from no effect (0.01 ± 0.12 years) in 2014 to 0.41 ± 0.15 years in 2017, and the dominance effect from −0.25 ± 0.16 years in 2014 to 0.19 ± 0.22 years in 2017 (Figure 3b; Table S12). After accounting for uncertainty in the estimates, the additive effect varied by a standard deviation of 0.10 years and the dominance effect by 0.07 years (60% and 86% of the variance was due to uncertainty in the additive and dominance effect, respectively). Three out of 10 pairwise differences between years in the additive effect, and none of the pairwise differences between years in the dominance effect, were statistically significant (Tables S13 and S14). In males, all variation among years in additive and dominance effects of *six6* was explained by uncertainty in the estimates (the $\overline{SE^2}$ was equal to or exceeded the observed variance), and there were no statistically significant differences between years in neither additive nor dominance effect (Tables S15 and S16).

Single-locus evolvability of *vgll3* varied among years, from 0.01% to 1.13% in females and from 0.35 to 2.50% in males (Figure 2c), while single-locus evolvability of *six6* ranged from 0.03 to 0.69% in females and from 0 to 0.15% in males (Figure 3c). This was further substantiated by the relatively high error-corrected standard deviations of these evolvabilities (Figures 2c and 3c), except for *six6* in males where there was no variation in genetic effects among years (Figure 3c).

4 | DISCUSSION

We found that average number of years spent at sea before maturation (sea age) varied among years within a population of Atlantic salmon and that part of the temporal variation in age at maturity was explained by variation in genotype frequencies at two major effect loci; *vgll3* and *six6*. Furthermore, genetic effects of *vgll3* and *six6* varied among years, suggesting that genotypes may differ in their response to the environment across years.

We found a strong average effect of *vgll3* on individual sea age in both females and males and a weaker average effect of *six6*. Previous studies have shown that *vgll3* and *six6* can have strong effects on sea age at maturity in Atlantic salmon (Ayllon et al., 2015; Barson et al., 2015; Besnier et al., 2023; Sinclair-Waters et al., 2022). Variation in genotype frequencies explained as much as 28% (females) and 16% (males) of the variation in average sea age among years, suggesting fluctuating contemporary evolution of sea age on a short time scale. Previous studies on Atlantic salmon have shown that sea age at maturity can evolve rapidly in response to changes in the environment and that these evolutionary changes were largely mediated by the *vgll3* (Czorlich et al., 2018; Jensen et al., 2022) and *six6* (Jensen et al., 2022) genomic regions. The average single-locus evolvability for *vgll3* was in the same order of magnitude as the median evolvability of life-history traits of 0.86% (Hansen & Pélabon, 2021). Considering

that sea age is controlled by many more genes than *vgll3* and *six6* (Sinclair-Waters et al., 2022), our results suggest that sea age at maturity of the salmon population in River Surna harbours substantial evolvability. Indeed, by assuming a heritability of 0.5, our estimates of total evolvability of sea age were around four (females) and nine (males) times higher than the median evolvability of life-history traits.

We show that genetic effects can vary considerably among years, which has not been accounted for in previous studies on the roles of *vgll3* and *six6* in the evolution of sea age in Atlantic salmon. For example, for males migrating to sea in our study river in 2015, there was more than a year difference in sea age between the youngest and oldest genotype and complete dominance for early maturation. In the following smolt cohort (2016), there was less than half a year difference between the youngest and oldest genotype, and no dominance for early or late maturation. Our results are in line with a previous study showing different effects of *vgll3* and *six6* on sea age when comparing two time periods (1983–1984 vs 2013–2016; Besnier et al., 2023). Temporal variation in genetic effects can be an important part of the evolutionary dynamics in Atlantic salmon because variation in additive and dominance effects affects the potential for sea age at maturity to evolve. Evolutionary potential depends on the additive genetic variance, which in turn depends on functional genetic effects (Álvarez-Castro & Carlborg, 2007; Lynch & Walsh, 1998). This is illustrated by the relatively high variation among years in single-locus evolvability estimates. For example, based on the average single-locus evolvability of *vgll3* in males (1.16%) and its among-year standard deviation (0.32%), the contribution of *vgll3* to the per cent increase in mean sea age under strong selection (i.e. a mean-standardized selection gradient = 1) is expected to vary between 0.84% and 1.48% per generation. The stability of genetic variances has been a subject of much research because of their importance for predicting evolutionary response (e.g. Arnold et al., 2008; Bégin & Roff, 2003; Björklund et al., 2013; Garant et al., 2008). Or study adds to this body of literature and highlights the potential importance of temporal variation in the functional genetic effects of large-effect genes.

Variation in genetic effects among some years may reflect genotype–environment interaction, whereby genotypes respond differently to changes in the environment across years. If we assume that variation in sea age among years reflects phenotypic plasticity, our results indicate that genotype differences in plasticity at both *vgll3* and *six6* can be substantial. In males, the error-corrected among-year variance in sea age for the *vgll3* LL genotype was more than three times that of the *vgll3* EE genotype, while in females, the *six6* EE genotype had nine times higher variance compared with the *six6* LL genotype. However, parts of the variation in sea age among years may reflect variation in the genotype frequencies of other genes. Genotype–year interactions may arise if there are epistatic interactions between *vgll3*/*six6* and other genes, and the frequencies of these genes vary among years. Yearly variation in linkage disequilibrium with other genes could also contribute to a genotype–year interaction. We cannot rule out the influence of additional genes based on our data. However, because experimental studies have shown that age at maturation depends on the environment in Atlantic salmon (food availability: Duston & Saunders, 1999; food quality and temperature: Jonsson et al., 2013), we expect sea age at maturity to be a plastic trait. This, taken together with the disproportionate large effects that *vgll3* and *six6* have on sea age compared with other loci (Sinclair-Waters et al., 2022), we consider it likely that the observed genotype–year interaction largely reflects genetic variation in plasticity.

Because this is an observational study based on salmon caught in recreational fishing, we cannot rule out effects, such as catchability or variation in fishing regulations, influencing our results. It is not unlikely that such factors influence estimates of average sea age. However, for such effects to influence our main results (genotype–year interaction), catchability or effects of fishing regulations would have to differ among genotypes.

Because our data are limited to fish that survived their marine migration, variation among years in mean sea age of genotypes reflects both variation in maturation strategy and in the relative survival of fish with different maturation strategies. However, in both cases, our results reflect differences between genotypes in how they respond to the environment. For example, genotypes may differ in risk-taking behaviour, which, depending on the environment, may be successful or not. This may in turn generate variation among genotypes in both survival and age-specific maturation probabilities.

Genotype–environment interaction is commonly studied by estimating differences between genotypes in reaction-norm slopes in relation to a specific environmental variable (Hutchings, 2011; Schlichting & Pigliucci, 1998). However, the reaction-norm approach can fail to detect an existing genotype–environment interaction if the chosen environmental variable is a poor proxy for the actual environmental driver of plasticity (Ramakers et al., 2023). Our approach of using year as a proxy for the environment can serve as a first step to detect a potential genotype–environment interaction in the wild. The next step will be to identify the environmental driver of the genotype–environment interaction. We have limited knowledge on how *vgll3* and *six6* genotypes interact with specific environmental factors (Åsheim et al., 2023). One possible explanation for our findings is that *vgll3* genotypes differ in their response to environmental variation that influence body condition. Common garden studies on two-year-old male Atlantic salmon have found differences between *vgll3* genotypes in the effect of body condition on the probability of maturing (Åsheim et al., 2023), and in the seasonal variation in body condition (House et al., 2023). A study in the wild by Aykanat et al. (2020) showing differences between *six6* genotypes in sea age-dependent stomach fullness further suggests that genotypes may differ in feeding strategy in Atlantic salmon.

The evolution of adaptive phenotypic plasticity requires underlying genetic variation in plasticity (Scheiner, 1993). Our finding of genotype differences in plasticity therefore suggests that phenotypic plasticity in sea age has the potential to evolve as an adaptation in Atlantic salmon. However, because the genetic basis of plasticity in sea age includes genes that have a large effect on sea

age itself, plasticity in this trait may evolve indirectly via selection on its mean (cf. Via, 1993). Hence, adaptation of plasticity is not ensured even in the presence of underlying genetic variation as the indirect response to selection on mean sea age can be maladaptive. For example, increased fishing pressure is expected to select for earlier maturation (Heino & Dieckmann, 2008) and therefore select against late-maturing genotypes (LL). Selection against the *vgll3* LL genotype may indirectly select for decreased plasticity, as the *vgll3* LL was the genotype with the highest variation in sea age among years. For *six6*, however, the early-maturing genotype was the most variable, and increased plasticity may evolve as an indirect response.

Even if age is a continuous trait, age at maturity in Atlantic salmon is often studied as a threshold trait (Sinclair-Waters et al., 2020; Tréhin et al., 2020). The most common approach is to use a binomial model that contrasts fish with a sea age of 1 year with older fish. This is a sound approach, which relates to quantitative genetic threshold-trait models where the observed discrete phenotype is mapped onto a continuous unobserved liability scale (see Lynch & Walsh, 1998, chapter 25). However, it is important to realize that the choice of scale is not arbitrary. The results on plasticity and genotype–environment interaction strongly depend on scale (Reid & Acker, 2022). The same goes for results and interpretation of genetic effects (Pavlicev et al., 2010) and therefore also the evolvabilities (see Houle et al., 2011 for a general discussion on the matter of measurement scale). Here, we have chosen to study sea age at maturity on the original scale. First, because it captures the complete variation in the trait (i.e. all observed sea ages: 1–5 years) in one variable, and second, because we find the results easier to interpret biologically on the original scale compared with, for example, the liability of spending more than 1 year at sea.

Overall, our results suggest a highly dynamic system of genetic variation and genotype–environment interactions in determining sea age at maturity in Atlantic salmon. Considering the importance of age at maturity for survival and reproduction, these dynamics likely play an important role in local adaptation and population demography. The large variation in sea age at maturity observed among populations of Atlantic salmon is associated with *vgll3* and *six6* allele frequencies and is believed to be shaped by local adaptation to the home river (Barson et al., 2015). Our observation of genotype differences in plasticity in the River Surna raises the question of whether there are genetic differences between populations, not only in mean sea age but also in their plastic responses to environmental changes. Genetic variation in phenotypic plasticity should therefore be considered when predicting population responses to environmental changes.

AUTHOR CONTRIBUTIONS

A.R., G.H.B. and L.P. contributed to conceptualization. O.U., P.F. and S.K. contributed to data curation. A.R. contributed to formal analysis, project administration and visualization. O.U., S.K., P.F., E.B.T., G.H.B. and L.P. contributed to funding acquisition. A.R., G.H.B. and Y.C. contributed to methodology. A.R. and G.H.B. contributed to validation. G.H.B, E.B.T. and Y.C. contributed to supervision. A.R. (lead), G.H.B., L.P. and E.B.T. contributed to writing—original draft. A.R. (lead), L.P., Y.C., O.U., P.F., E.B.T., S.K. and G.H.B. contributed to writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and scripts used to generate the results in this study are available at Zenodo via the following URL: https://doi.org/10.5281/zenodo.8393404.

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SUPPORTING INFORMATION

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