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Overruled by nature: A plastic response to environmental change disconnects a gene and its trait

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Abstract

In Atlantic salmon, age at maturation is a life history trait governed by a sex-specific trade-off between reproductive success and survival. Following environmental changes across large areas of the Northeast Atlantic, many populations currently display smaller size at age and higher age at maturation. However, whether these changes reflect rapid evolution or plasticity is unknown. Approximately 1500 historical and contemporary salmon from the river Etne in Western Norway, genotyped at 50,000 SNPs, revealed three loci associated with age at maturation. These included *vgll3* and *six6* which collectively explained 36%–50% of the age at maturation variation in the 1983–1984 period. These two loci also displayed sex-specific epistasis, as the effect of *six6* was only detected in males bearing two copies of the late maturation allele for *vgll3*. Strikingly, despite allelic frequencies at *vgll3* remaining unchanged, the combined influence of these genes was nearly absent in all samples from 2013 to 2016, and genome-wide heritability strongly declined between the two time-points. The difference in age at maturation between males and females was upheld in the population despite the loss of effect from the candidate loci, which strongly points towards additional causative mechanisms resolving the sexual conflict. Finally, because admixture with farmed escaped salmon was excluded as the origin of the observed disconnection between gene(s) and maturation age, we conclude that the environmental changes observed in the North Atlantic during the past decades have led to bypassing of the influence of *vgll3* and *six6* on maturation through growth-driven plasticity.

KEYWORDS
phenotypic plasticity, salmon maturation, sexual conflict, six6, vgll3

1 | INTRODUCTION

Understanding the mechanisms by which organisms adapt to their environments is a central question in biology (Andrew et al., 2013; Losos, 2000). However, beyond the academic curiosity that motivates biologists to investigate how species evolved and adapted until now, accelerating climate change and ongoing habitat destruction catalyses a sense of urgency when considering the fate of many species in the future. As unprecedentedly fast environmental changes have occurred for many taxa during the last half century (Chevin et al., 2010; Dullinger et al., 2012; Pörtner et al., 2022), the current mechanisms of adaptation of many species may not couple with the pace at which environmental change is now occurring, leading thus to population declines and extinctions. Consequently, the mechanisms

of adaptation and their potential to remain effective in a context of rapidly changing environment are becoming increasingly important to understand (Bandillo et al., 2017; Candolin & Heuschele, 2008; Garcia de Leaniz et al., 2007; Kwan et al., 2008).

In the context of environmental change, genes associated with sexual conflicts (Parker, 1974) are of particular interest. Sexual conflicts are associated with sex-specific selection and therefore expected to promote genetic diversity in the underlying genes (Rowe et al., 2018). Although theoretical models suggest this only applies if selection magnitude is asymmetrical between sexes (McGlothlin et al., 2019), sexual conflicts have the potential to help maintain standing genetic variation on important fitness traits within the population. An illustration of this occurs in anadromous Atlantic salmon (*Salmo salar* L.) where a single gene (*vgll3*) is strongly associated with the age at maturation, a highly adaptative trait subject to sexual conflict (Ayllon et al., 2015; Barson et al., 2015). In many species, age at maturation represents a trade-off, as late-maturation gives larger body sizes and thus higher reproductive success, but at the increased risk of dying before reproduction (Fleming & Einum, 2011). In Atlantic salmon, the optimum value for this trait differs between the sexes, as males mature earlier and smaller whereas females benefit from later maturation and a larger body size resulting in more and larger eggs (Fleming & Einum, 2011). This sexual conflict is in part resolved by the mediation of *vgll3* (Barson et al., 2015) through sex-specific dominance.

Studies of *vgll3* and age of maturation in Atlantic salmon have resulted in inconstant estimations regarding the degree to which this gene influences the trait. Several studies have demonstrated a very strong association in wild North European populations (Ayllon et al., 2015; Barson et al., 2015; Czorlich et al., 2018; Jensen et al., 2022), but in stark contrast, little or no association has been observed in wild populations in North America (Boulding et al., 2019; Mohamed et al., 2019). Furthermore, conflicting observations have also been reported in domesticated Norwegian farmed strains reared under aquaculture conditions (Ayllon et al., 2019; Sinclair-Waters et al., 2020). This begs the question, why does the influence of *vgll3* on age at maturation vary so greatly?

Salmonids have been exposed to a wide range of anthropological challenges including habitat modifications since the Industrial Revolution (Forseth et al., 2017). Furthermore, during the past two decades, most salmon populations in the North Atlantic have shifted towards later maturation (Otero et al., 2012; Vollset et al., 2022) and smaller size at age (Bal et al., 2017; Quinn et al., 2006; Todd et al., 2021; Vollset et al., 2022). These changes are thought to be linked to changing oceanic conditions, and in particular, the ecological regime-shift observed in 2005 (Vollset et al., 2022). However, whether the observed changes in age at maturation within salmon populations reflects rapid evolution or plastic responses to these changing oceanic conditions, is currently unknown. The same trends towards later maturation have also been documented in the salmon population inhabiting the river Etne on the west coast of Norway, where the proportion of fish maturing after 1 year at sea dropped from 63% in the period 1983–1984 to 34% in 2018–2019 (Harvey

et al., 2022). The primary objective of the present study was to investigate whether the observed changes in age at maturation in the salmon population in the river Etne were the result of phenotypic plasticity, or alternatively, evolution in the gene(s) influencing this trait. To address this, we genotyped historical (early 1980s) and contemporary (mid 2010s) samples with a 50k panel of genome-wide SNPs. This approach revealed the dissociation between age at maturation and two loci, *vgll3* and *six6*, that explained 36%–50% of the variation in the 1983–1984 period, but only 7% in the most recent samples.

2 | MATERIALS AND METHODS

2.1 | Samples

This study is based on samples obtained from adult salmon captured in the river Etne, in western Norway, 60° N. This river is home to a salmon population of typically 1000–2500 adults returning from the sea annually (Harvey et al., 2017). A permanent trapping facility installed in the river has permitted sampling almost the entire adult spawning population since 2013, which facilitated access to both an extensive set of DNA samples, as well as to phenotypic and phenological data. For the present study, 797 wild adult salmon captured in the 1983–1984 angling season were compared to 751 wild adult salmon captured in the upstream fish trap in the period 2013 to 2016 (Besnier et al., 2022). For the contemporary samples (2013–2016), an estimation of individual genetic admixture was computed as the proportion of domestic ancestry in each individuals genome (see Besnier et al., 2022 for details). In addition, a sample of 350 domesticated farmed salmon escapees that were removed from the river in the period 1989–2012 (15 per year), were genotyped with the same set of markers.

2.2 | Genotyping and sex determination

All samples were genotyped on a ThermoFisher Axiom 57 K single nucleotide polymorphism (SNP) array (NOFSAL03, 55,735 markers) developed by Nofima (Norwegian institute for applied research in food aquaculture and fisheries) in collaboration with private aquaculture companies Mowi and SalmoBreed (Besnier et al., 2022). SNPs were checked following the "Best Practice Workflow" on the Affymetrix axiom analysis software (available at: https://www.thermofisher.com/no/en/home/technical-resources/software-downloads.html). SNPs with call rates lower than 0.97 and samples with call rates lower than 0.85 were discarded, whereas markers classified as "PolyHighResolution" (high resolution in both homozygous and heterozygous clusters) were conserved for further data analysis. Due to lower DNA quality of the historical samples, nearly 50% of the SNPs displayed a call rate value below the recommended threshold (0.97). The remaining 50% SNPs fulfilled the recommended criterion. After quality

checking, this approach resulted in 22,571 PolyHighResolution SNPs that were used in the analysis.

Fish were sexed by examining variants of the sdY gene (Eisbrenner et al., 2014; Yano et al., 2012); that is, males were identified based on the presence of exons 2 and 4. Samples were genotyped on an Applied Biosystems ABI 3730 Genetic Analyser, and genotypes were called using GeneMapper (Applied Biosystems, version 4.0). The analysis of the sdY gene provides an accurate identification of sex, although, a very low percentage of fish identified as genetic males are phenotypic females due to carrying an inactive pseudo-copy of the sdY gene with both exon 2 and 4 (Ayllon et al., 2020).

2.3 | Genome scan for loci associated with age at maturation

Age at maturation was modelled as a binary trait consisting of early maturing fish, that is, fish returning after one sea-winter (1SW), also known as grisling, versus late maturing fish, that is, fish returning after two or more winters at sea (2$^+$SW). The probability of maturing early was then modelled in a generalized linear model with logit link function:

$$\log\left(\frac{P_{(e)}}{1 - P_{(e)}}\right) = G_i + sex + year + e \qquad \text{(Model 1)}$$

where $P_{(e)}$ is the probability of early maturing, G_i is the SNP genotype at locus i, sex is a binary factor accounting for genetically determined sex, $year$ is a factor accounting for the sampling year, and e a normally distributed vector of residuals. Significance of association between genotype and sea age was estimated by comparing the deviance of model 1 with the deviance of the model without genetic effect. The difference was compared to a chi-squared distribution with one degree of freedom. Model 1 was fitted at each SNP available on the data set, and the obtained p-values were adjusted for multiple testing by following Bonferroni correction. All p-values given in the genome scan result section are corrected for multiple testing.

2.4 | Haplotyping

Haplotypes were reconstructed using the PHASE 2.1 software (Stephens et al., 2001) in the historical and contemporary data separately. Two loci on SSA9 and SSA25 were more specifically considered for haplotype reconstruction as they displayed high association with age at maturation, and associated genes vgll3 and six6 were previously described in the same two genomic regions (Ayllon et al., 2015; Barson et al., 2015; Czorlich et al., 2018). On SSA25, a haplotype window consisting of four polymorphic SNPs (AXE-87309414, AXE-172546510, AXE-87309615, AXE-87420691) was reconstructed in the region spanning from 28.65 to 28.66 Mb

containing vgll3 (https://www.ncbi.nlm.nih.gov/gene/106586514). On SSA09, a haplotype window consisting of three SNPs (AXE-172546568, AXE-88029383, AXE-87668000), spanning from 24.86 to 24.95 Mb was reconstructed around the position of six6 (https://www.ncbi.nlm.nih.gov/gene/106610974).

2.5 | Statistical analysis

2.5.1 | Genetic structure to age at maturation variation

Due to the sex specific dominance observed in vgll3, the genetic structure was estimated for males and females separately. The probability of early maturation was modelled as a response to additive and dominance genetic effects as follow:

$$\log\frac{P_{(e)}}{1 - P_{(e)}} = a_i + d_i + year + e \qquad \text{(Model 2)}$$

where $P_{(e)}$ is the probability of early maturing, a_i and d_i are respectively the additive and dominance effects at locus i, $year$ is a factor accounting for the sampling year, and e a normally distributed vector of residuals. The model was fitted in a GLM with logit link function in R (R Core Team, 2022), and the variance contribution was deduced from the difference in model deviance between model 2 and a model that only accounted for capture year. Two loci interaction models were tested similarly by accounting for the additional interaction parameters between loci $_i$ and $_j$. In contrast with the genome scan, the test for significance of the different genetic parameters were not corrected for multiple testing. All p-values given with the estimation of genetic effect are nominal values.

Heritability for age at maturation was estimated by computing the polygenic contribution to the trait from the following model:

$$\log\frac{P_{(e)}}{1 - P_{(e)}} = sex + year + a + e$$

where a is the normally distributed polygenic contribution $a \sim N(0, G\sigma_a^2)$. The variance explained by all SNPs was computed by the GREML function from GCTA software (Lee et al., 2011; Yang et al., 2010), and were used to estimate the polygenic contribution and heritability. Heritability was computed from all SNPs excluding markers linked with the vgll3 and six6 loci.

2.5.2 | Comparison in age at maturation

Potential differences in age AT maturation between historical and contemporary samples was tested by chi-squared test on a contingency table reporting the number of observed 1, 2 and 3+ sea winter adults within historical and contemporary samples.

Phenotype	Mean value (cm) 1983–1984	Mean value (cm) 2013–2016	df	t-test	p-value
Females					
First sea winter length	47.2	41.7	500	14	<.001
1SW adult length	55.1	55.0	37	0.89	.37
2SW adult length	79.4	75.3	202	5.50	<.001
Males					
First sea winter length	45.4	41.0	711	13.2	<.001
1SW adult length	55.6	56.8	441	2.7	.007
2SW adult length	80.6	72.6	85	5.4	<.001

TABLE 1 Comparison of fish length between historical and contemporary samples during first winter at sea (immature fish), adult maturing after one sea winter (1SW), and adult maturing after two winters at sea (2SW).

Note: For each comparison, we report the statistics for testing the difference between historical and contemporary samples with a two-sided *t*-test: degree of freedom (df), *t*-test value (*t*), and *p*-value (*p*).

2.5.3 | Size at age

Individual body length was recorded for every fish passing the trap in the contemporary sample, whereas the adult length of the 1983–1984 fish were calculated from reading scales samples. In addition, the growth at first sea winter was estimated for both historical and contemporary samples by calculating length at first sea winter from reading scales. The difference in length between samples from 1983 to 1984 and from 2013 to 2016 was tested with a two-sided *t*-test, separately for each sea-age and sex categories.

2.5.4 | Potential role of admixture

The salmon population in the river Etne has been subject to introgression from domesticated salmon escaping from commercial fish farms, with an average 24% of genetic admixture in the contemporary population (Besnier et al., 2022; Glover et al., 2013; Karlsson et al., 2016). Individual admixture with domesticated salmon has already been correlated with earlier adult maturation in this population (Besnier et al., 2022). Therefore, in order to account for the potential influence of admixture on the temporal influence of loci on age at maturation in this population, we investigated whether the change in genetic architecture of age at maturation could be linked to genetic admixture.

A third model was fitted with the aim to evaluate a potential interaction between admixture and *vgll3* or *six6* genotypes.

$$\log \frac{P_{(e)}}{1 - P_{(e)}} = a_i * admix + d_i * admix + year + e \quad \text{(Model 3)}$$

where *admix* is the individual genetic admixture as computed in Besnier et al. (2022).

In addition, to investigate the cause of the observed temporal change in the *six6* allelic frequency, we also split the contemporary samples according to individual admixture, thus creating
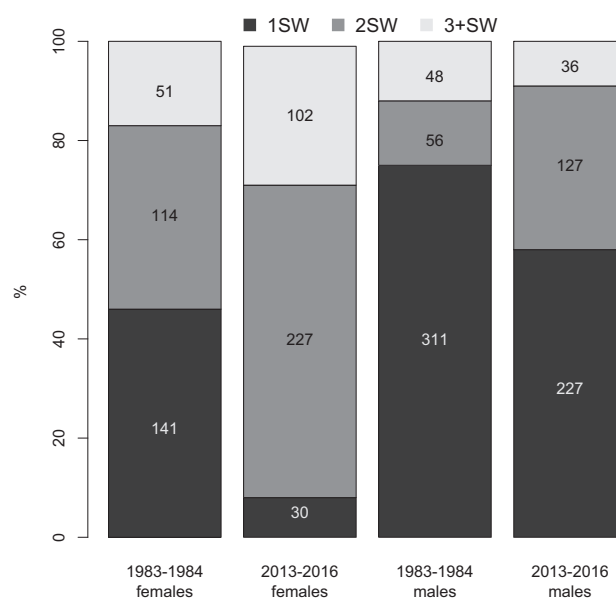
FIGURE 1 Distribution of age at maturation between 1, 2 and 3+ sea winters in the male and female samples from 1983 to 1984 and 2013 to 2016.

a group of highly admixed fish (admixture >0.3, N = 233) and a group of low admixed fish (admixture <0.15, N = 221). The *six6* allelic frequencies were compared between the two groups using chi-squared test.

3 | RESULTS

3.1 | Temporal changes in age and size at maturation

Marine growth was compared between the historical (1983–1984) and contemporary (2013–2016) samples. During this period, the length of the fish decreased significantly (*p* < .01) with

first sea winter length declining from 47.2 to 41.7 cm and from 45.4 to 41.0 cm for females and males, respectively. Similarly, the length of the two sea-winter (2SW) adults decreased from 79.4 to 75.3 cm and from 80.6 to 72.6 cm for females and males, respectively, while the length of the one sea-winter (1SW) adults remained stable (Table 1). During the same time period, we also observed a strong decline in the frequency of fish maturing after one winter at sea from 46% to 8% for the females ($\chi^2 = 120$, df = 1, $p < 2.10^{-16}$), and from 75% to 58% for the males ($\chi^2 = 25$, df = 1, $p = 4.10^{-7}$; Figure 1).

3.2 | Genome scans

The genome scan for age at maturation identified three loci displaying a significant association in the historical samples (Figure 2a,b), one on each of chromosomes SSA09, SSA24 and SSA25. The genomic regions identified in SSA25 and SSA09 overlapped with loci previously described as major contributors to the sea age variability in salmon: *vgll3* on SSA25 and *six6* located on SSA09. In the contemporary samples, the association was substantially weaker (Figure 2c,d). The degree of association between age at maturation and these genomic regions was investigated further in the historical and contemporary data set.

3.3 | *vgll3* and *six6* haplotypes

Haplotypes were reconstructed in the historical and contemporary samples separately, across the genomic regions in SSA25 and SSA9 that contained the *vgll3* and *six6* genes respectively. On SSA25, two haplotypes were predominant in the historical samples with frequencies of 56% and 39% (Table 2) and respectively associated with early and late sea age. The mean sea age was 1.18 for the homozygous haplotype "1221", and 2.46 for the homozygous haplotype "2112", which will thus be referred to as *vgll3*-E (early maturation) and *vgll3*-L (late maturation) alleles from hereon. In the contemporary samples, the same two haplotypes were found in almost identical frequencies (df = 1, $\chi^2 = 0.85$, $p = .35$) to the historical samples (59% and 39% for *vgll3*-E and *vgll3*-L, respectively). This demonstrates that no temporal change in the haplotype frequencies occurred at this locus during the three-decade period, despite the observed change in the population's age of maturation.

The mean age at maturation in each genotype class (Figure 3) displayed a strong association with an additive effect of *vgll3* on female sea age in the historical data (Figure 3a, Table S1–S3), whereas association of *vgll3* almost disappeared in the contemporary female data (Figure 3c, Table S1–S3). For the historical male data (Figure 3b, Table S1–S3), a strong *vgll3* association with a dominant *vgll3*-E allele was also detected, whereas the genetic association was strongly reduced in the contemporary data (Figure 3d, Table S1–S3).
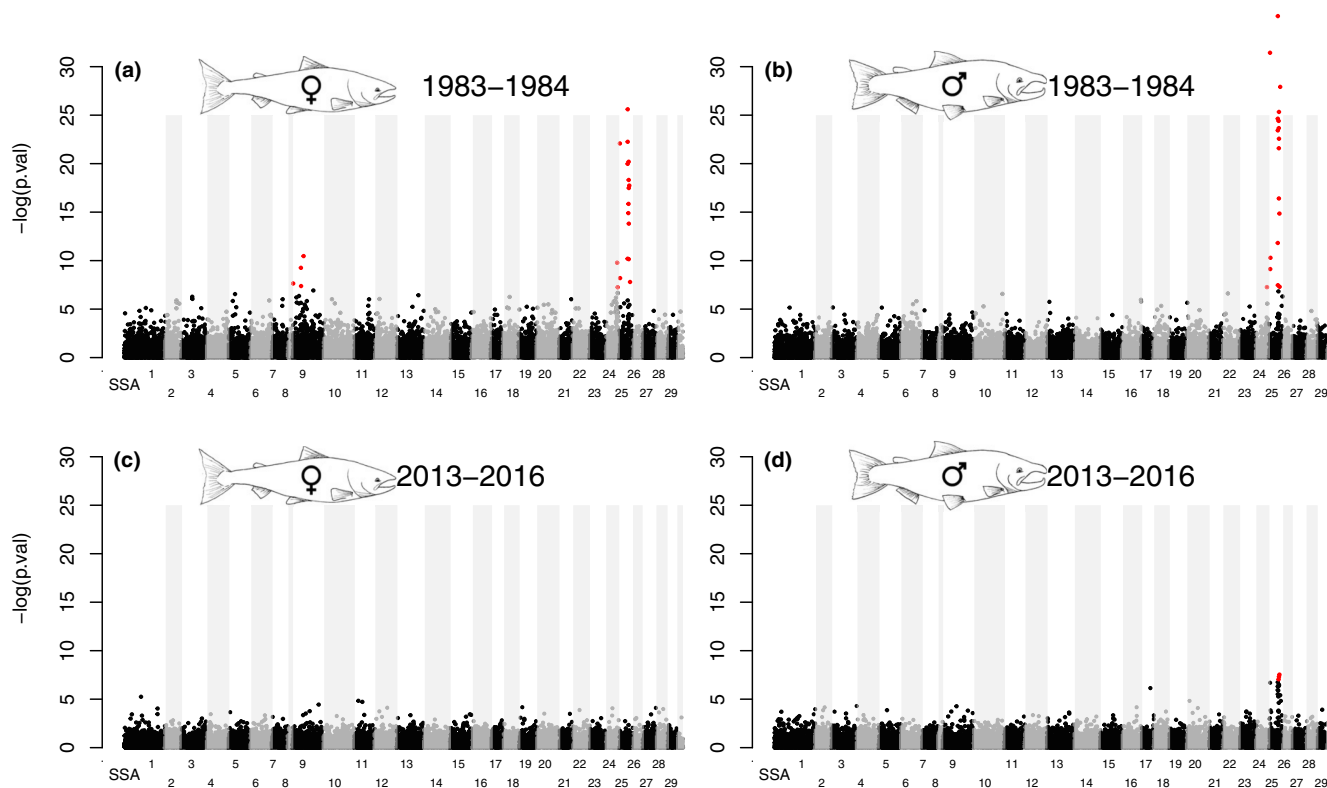

FIGURE 2 Scan for single nucleotide polymorphism (SNP) association with age at maturation. Red dots represent SNPs with significant association with sea age (*p* < .01 after correction for multiple tests). (a) Females from 1983 to 1984, (b) males from 1983 to 1984, (c) females from 2013 to 2016 and (d) males from 2013 to 2016. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Observed occurrences of each haplotype per sex and associated mean sea age (M.S.A) in the historical, contemporary and farmed samples.

| Haplotypes | 1983–1984 | | | | 2013–2016 | | | | Farmed | |
| | Females | | Males | | Females | | Males | | Females | Males |
	%(N)	M.S.A	%(N)	M.S.A	%(N)	M.S.A	%(N)	M.S.A	%(N)	%(N)
vgll3										
1221	$59_{(364)}$	1.2	$54_{(455)}$	1.1	$61_{(438)}$	2.2	$58_{(454)}$	1.4	$53_{(93)}$	$63_{(264)}$
1222	$0_{(0)}$	NA	$0_{(1)}$	NA	$0_{(0)}$	NA	$0_{(1)}$	NA	$0_{(0)}$	$0_{(0)}$
1111	$1.5_{(9)}$	NA	$2_{(17)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	$0_{(1)}$
1112	$0_{(1)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	NA	$0_{(1)}$	NA	$0_{(0)}$	$0_{(1)}$
2221	$1_{(9)}$	NA	$2_{(18)}$	NA	$1_{(9)}$	NA	$1(13)$	NA	$3_{(5)}$	$5_{(24)}$
2222	$0_{(0)}$	NA	$0.5_{(3)}$	NA	$0_{(3)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	$0_{(0)}$
2111	$1.5_{(5)}$	NA	$0.5_{(4)}$	NA	$0_{(0)}$	NA	$1_{(0)}$	NA	$0_{(0)}$	$0_{(1)}$
2112	$37_{(230)}$	2.5	$41_{(344)}$	2.5	$38_{(272)}$	2.5	$40_{(309)}$	2.2	$44_{(76)}$	$31_{(128)}$
six6										
111	$41_{(256)}$	1.4	$40_{(337)}$	1.2	$23_{(166)}$	2.3	$25_{(195)}$	1.6	$16_{(29)}$	$14_{(65)}$
112	$0_{(3)}$	NA	$1_{(8)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	NA	$0_{(0)}$	$0_{(0)}$
121	$24_{(146)}$	2.5	$27_{(225)}$	1.5	$31_{(227)}$	2.4	$35_{(275)}$	1.5	$42_{(76)}$	$44_{(194)}$
122	$21_{(127)}$	2.3	$19_{(160)}$	2.0	$29_{(209)}$	2.6	$26_{(203)}$	1.4	$26_{(48)}$	$26_{(115)}$
211	$12_{(73)}$	1.6	$12_{(100)}$	1.2	$11_{(80)}$	2.3	$10_{(80)}$	2.0	$2_{(3)}$	$2_{(8)}$
221	$1_{(8)}$	NA	$1_{(11)}$	NA	$4_{(28)}$	NA	$3_{(25)}$	NA	$14_{(26)}$	$14_{(62)}$
222	$1_{(5)}$	NA	$0_{(1)}$	NA	$2_{(12)}$	NA	$1_{(2)}$	NA	$0_{(0)}$	$0_{(0)}$

Note: M.S.A is calculated as mean sea age of the samples that are homozygous for the haplotype.

On SSA09, four main haplotype sequences linked to the *six6* gene were predominant in both historical and contemporary samples (Table 2). With a respective sea age of 1.3 and 1.4 years for the homozygous fish in the historical samples, both "111" and "211" haplotypes were assigned to the early variant of *six6*, whereas haplotypes "121" and "122", with a respective mean sea age of 1.9 and 2.1 years, were assigned to the late variant. Following this, we observed an increase in the frequency of the *six6* late variant, from 44% in the historical samples to 60% in the contemporary samples (df = 1 $\chi^2 = 111$, $p < 2.2 \cdot 10^{-16}$). The mean age at maturation in each genotype class (Figure 3) showed an additive effect of *six6* in the historical female data (Figure 3a, Table S2), and historical male data (Figure 3b Table S2). In contrast, we did not observe any association between *six6* and sea age in the contemporary data (Figure 3c,d, Table S2).

Cumulatively, *vgll3* and *six6* accounted for 50% of the model deviance in the historical male data set and 36% in the historical female data set. In stark contrast, the cumulative effect of the same loci only accounted for 7% and 3% of the model deviance in the contemporary male and female data sets, respectively. In the same time interval, the polygenic genome-wide contribution to age at maturation, excluding *vgll3* and *six6*, also decreased with an estimated heritability of 0.82 ± 0.05 in the historical data set and 0.44 ± 0.1 in the contemporary data set.

Testing the interaction between these two loci revealed significant departure from additivity between *vgll3* and *six6* in the males of the historical samples (Table S3). This interaction is illustrated in Figure 3b where the *six6* genotype is only associated with age at maturation for the samples that are homozygous for the *vgll3-L* allele. No significant departure from additivity was observed in the historical females (Table S3).

3.4 | Genetic admixture

The salmon population inhabiting the river Etne has been subject to introgression from domesticated farmed escapees. We therefore tested whether the observed temporal change in genetic architecture of age at maturation could be linked to admixture with farmed fish. When predicting age at maturation from the joined effect of admixture and genotype, no interaction was detected between individual admixture and *vgll3* genotype ($\chi^2 = 3.6$, df = 2, $p = .161$), nor between individual admixture and *six6* genotype ($\chi^2 = 2.7$, df = 2, $p = .24$), indicating that the temporal dissociation between these loci and age at maturation was independent from individual admixture.

To investigate the cause of the change in *six6* allelic frequency, the contemporary samples were split according to individual admixture. The frequency of the late allele was 63% among the high admixed fish and only 52% among the low admixed fish ($\chi^2 = 10.8$, df = 1, $p < .01$) indicating that admixture from farmed escapees is a likely contributor to the observed change in *six6* allelic frequency in the population. However, with a documented average of 24% genetic admixture from farmed escapees in the river Etne population,
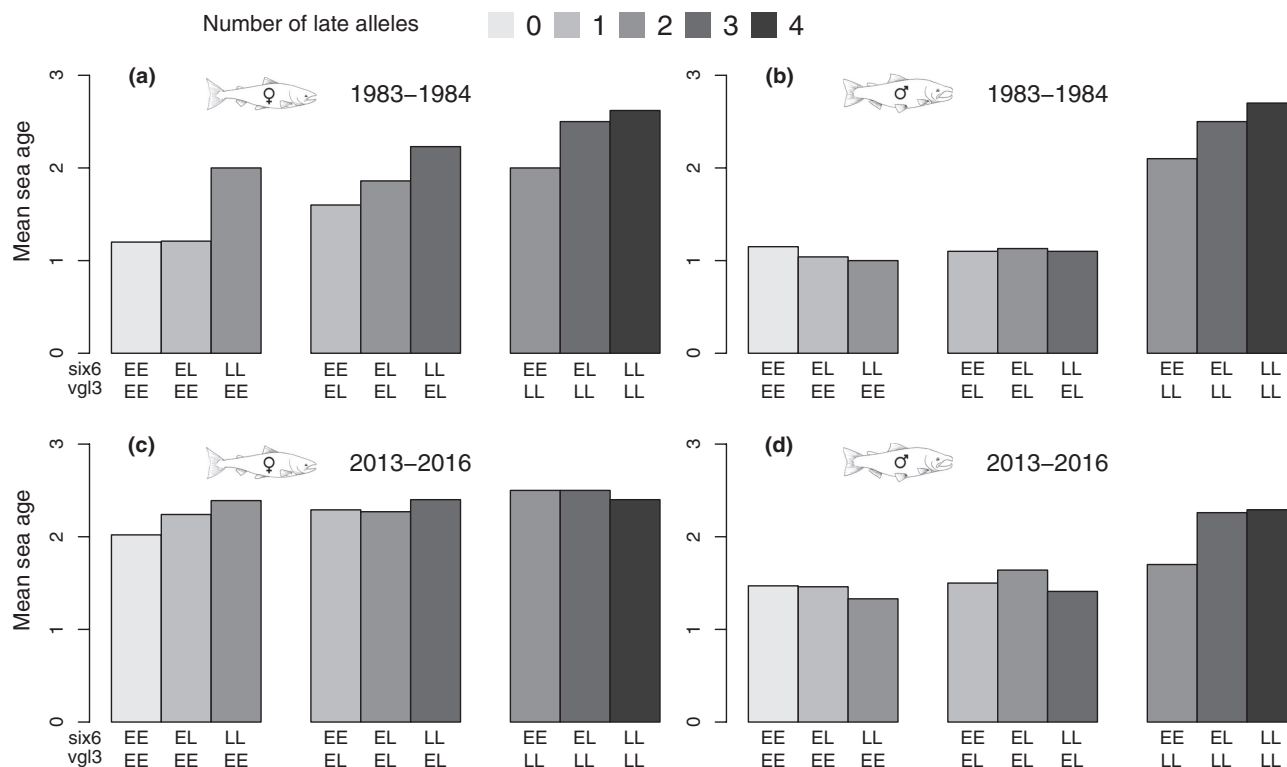
FIGURE 3 Mean sea age of the samples for each class of genotypes at *vgll3* and *six6*. (a) Females from 1983 to 1984, (b) males from 1983 to 1984, (c) females from 2013 to 2016 and (d) males from 2013 to 2016.

admixture alone is only expected to cause an increase in the *six6* late allele frequency from 44% in the historical (nonadmixed) population, to 48% in the contemporary (admixed) population. This is lower than the observed change to 60%.

4 | DISCUSSION

We document a temporal dissociation between age at maturation in a population of Atlantic salmon and the genotypes of three loci, including the previously identified candidate genes *vgll3* and *six6* (Ayllon et al., 2015; Barson et al., 2015; Czorlich et al., 2018). This dissociation was observed in samples separated by a 30-year time interval and was accompanied by an increase in the frequency of the late maturing allele at the *six6* locus for both males and females, while no change was observed at the *vgll3* locus. The salmon population in the river Etne has been subject to introgression from domesticated salmon escaping from commercial fish farms, with an average 24% of genetic admixture in the contemporary population (Besnier et al., 2022; Glover et al., 2013; Karlsson et al., 2016). However, no interaction was found between individual admixture and the effects of *six6* or *vgll3* on age at maturation. Furthermore, admixture with farmed escapees in this river is associated with increased marine growth rate and earlier age at maturation (Besnier et al., 2022), whereas the temporal trend for this population is a decline in marine growth rate and a marked increase in age at maturation (Harvey et al., 2022). For these reasons, admixture with farmed escapees is

discarded as a major factor causing the temporal disassociation between these genes and age at maturation.

In the historical data from 1983 to 1984, the combined effect of *vgll3* and *six6* was not fully additive. Epistatic interaction was detected in the samples of males where the effect of *six6* alleles was only visible for the group of individuals bearing two copies of the late *vgll3* allele. This may be connected to the dominance of *vgll3*-E allele in the males, where one copy of early allele at the vgll3 locus is enough to force early maturation, thus overriding any *vgll3*-L and possibly *six6*-L allele as well. *six6* was previously identified as a candidate locus associated with age at maturation (Barson et al., 2015), but little is known about the genetic effects of this locus. The work presented here is the first to document a sex-specific interaction between *vgll3* and *six6*.

In the river Etne, the frequency of late maturing fish is higher among females than among males. This difference is assumed to be the result of adaptation to sexual conflict where the advantage of maturing late is greater for females than for males (Fleming & Einum, 2011). With the *vgll3*-E allele being dominant in males only, *vgll3* is believed to play a key function in the resolution of sexual conflict in the optimal age of maturation in salmon (Barson et al., 2015). However, with the present results documenting the almost complete dissociation between age at maturation and *vgll3* genotypes in parallel with a trend towards later maturation strategy in both sexes simultaneously, the perennity of local adaptation in the population inhabiting the river Etne can be questioned. Noteworthy, sex-specific strategies of maturation seem to perdure in the population

despite the population's overall increase in age at maturation, and importantly, *vgll3*'s contribution being almost completely eradicated in the contemporary samples. In fact, the difference in early-maturation frequencies between males and females increased in the contemporary data set, strongly suggesting that other mechanisms are acting instead of, or in parallel with *vgll3*, to maintain sex specific age at maturation. This hypothesis is consistent with the description of multiple loci associated with age at maturation (Sinclair-Waters et al., 2020).

Vgll3 and age at maturation was also associated in Canadian salmon populations (Kusche et al., 2017). However, the absence of association in multiple North American populations (Boulding et al., 2019; Mohamed et al., 2019) suggested that *vgll3* is not the only regulator of sexual conflict for age of maturation in Atlantic salmon. The present study confirms this observation and further shows that the relative influence of *vgll3* is not stable in time. In the case of the population in the river Etne, our data reveals that other unidentified factors also play a major role in maintaining the sex-specific differences in maturation strategies when the link between age at maturation and *vgll3* is disconnected.

The observed trend towards slower marine growth and later maturation in the population inhabiting the river Etne has also been reported in many other salmon populations in the North Atlantic (Bal et al., 2017; Otero et al., 2012; Quinn et al., 2006; Todd et al., 2021; Vollset et al., 2022). While the precise triggers and mechanisms underpinning to the development of sexual maturation are not yet fully understood in Atlantic salmon (Mobley et al., 2021), slow growth and late maturation is consistent with the hypothesis of size or perhaps growth-rate threshold as a determinant for salmon maturation (Rowe et al., 1991; Simpson, 1992; Taranger et al., 2010). Such an energy-budget threshold might also be genetically regulated through the mediation of *vgll3*, which has been shown to be linked with cell fat regulation (Halperin et al., 2013) or *six6* which has been linked to stomach fullness and prey composition (Aykanat et al., 2020). Following this hypothesis, slow growth due to environmental conditions, such as lack of prey, would lead to later maturation as a higher proportion of fish would fail to reach the weight (or growth-rate) threshold for maturation after one single year at sea. This hypothesis is also consistent with the observed decrease in heritability for age at maturation, illustrating that in the contemporary samples, this trait is more influenced by environmental factors, and less by genetic. This encompasses a reduction of the effect of single genes like *vgll3* and *six6*, as well as the general polygenic contribution.

Observations suggest important changes in oceanic conditions met by salmon migrating from the river Etne, and other salmon populations in this region, in the period 1980–2010 (Vollset et al., 2022). The initial marine migration route for salmon originating from populations on the west of Norway including the river Etne is probably northward through the southern Norwegian Sea (Gilbey et al., 2021). Here, changes in the oceanographic conditions have been reported in the last years. For example, water temperature increased by nearly 1°C at 50–200m depth from early 1980s until 2021, mainly due to warmer water masses flowing into the southern Norwegian

Sea (ICES, 2021a; Skagseth & Mork, 2012). The early 1980s are also considered as the end of "The great salinity anomaly", which was a period with large inflow of cold and fresh Arctic water into the Norwegian Sea. The large proportion of Arctic water entering the Norwegian Sea is correlated to increased productivity (Skagseth et al., 2022), and to improved feeding conditions for post-smolts in the region (Utne et al., 2022). Therefore, salmon returning in 1983 and 1984 had probably been feeding in a very productive sea during the initial post-smolt phase, whereas salmon returning to rivers in 2013–2016 had been feeding in a warm and saline Norwegian Sea. During this later period, observed stomach fullness and condition factor for post-smolt sampled in the Norwegian Sea were low (Utne, Díaz Pauli, et al., 2021). In addition, the potential interspecific competition with other pelagic fish for prey (Utne, Thomas, et al., 2021) was low in the early 1980s as the total biomass of pelagic fish feeding in the Norwegian Sea in 1982–1983 was around one-third of the total biomass in the period 2013–2016 (ICES, 2008, 2021b) when Norwegian Spring-spawning herring had not yet recovered from the collapse in the late 1960s, and NEA-mackerel and blue whiting stock biomasses were at low levels (ICES, 2008). Multiple independent observations therefore confirm that environmental conditions were less favourable for salmon growth in the last decade than in the early 1980s. It is thus conceivable that the changes observed in the salmon population inhabiting the river Etne are caused by environmental perturbations occurring in the sea and are thus likely to affect other salmon populations in this region.

Under commercial aquaculture conditions, farmed Atlantic salmon typically display early sexual maturation (Taranger et al., 2010), and importantly, the relative influence of *vgll3* on age at maturation appears to be largely bypassed through plasticity (Ayllon et al., 2019). Yet again, this response is sex-specific as a study conducted under aquaculture conditions (Ayllon et al., 2019) reported that *vgll3* did not show any correlation with age at maturation in females while displaying a weak association in males (Ayllon et al., 2019). The commercial farm strain used in the aforementioned study, known as Mowi, stemmed from wild Norwegian salmon populations in which *vgll3* was identified as a candidate gene for influencing age at maturation (Ayllon et al., 2015; Barson et al., 2015). The authors concluded that high calorie feed intake combined with artificial light and temperature regimes as well as potential genetic or epigenetic components, may alter the impact of *vgll3* on age at maturation (Ayllon et al., 2019). Anecdotally, it is also worth noting that despite multiple generations of directional selection against early maturing fish in the domesticated farmed salmon, the genetic variability of *vgll3* remains high in the Mowi strain (Ayllon et al., 2019). It is thus possible that a rapid change in environmental conditions, such as feed intake and therefore growth-rate, may bypass the effect of *vgll3* without letting selection alter the allelic frequencies of the gene.

Based upon the above discussion, we can hypothesize a two-threshold model where the effect of *vgll3* on age at maturation is bypassed when abundance of feed resources is very high, as in farming conditions, or when feed resources are very low and fish need

to spend more time at sea to acquire the necessary energy-reserves for maturation and reproduction. When resource availability falls between both thresholds, *vgll3* may play a more important role in determining age at maturation. Inversely if feed resources exceed the high threshold, or do not reach the low one, *vgll3* is bypassed by environmental conditions, and therefore age at maturation is determined by a combination of other genetic and environmental factors. Given the reduction in heritability for age at maturation described in this data, it is likely that the relative importance of environmental factors increases in this last scenario.

In the face of changing environmental conditions, one may expect the allelic frequencies at the associated loci to change in response to the newly induced selection pressure (Czorlich et al., 2018; Jensen et al., 2022). This is the case for *six6* where the temporal trend towards later maturation is accompanied by an increase of the *six6*-L allele frequency. This shift in allelic frequencies is probably due to positive selection on the *six6-L* allele in conjunction with admixture from spawning intrusion of domesticated farmed salmon escapees. In contrast, the *vgll3* allelic frequencies remained stable despite major changes in age at maturation in the population. This result strongly indicates that environmental conditions changed during the period 1985–2012, creating a situation where the influence of *vgll3* was effectively bypassed before natural selection had time to operate. In contrast, the change in allelic frequencies observed on the *six6* locus could not be solely explained by gene flow from domesticated salmon escapees, suggesting that selection had the time to modify the allelic frequencies at the *six6* locus before the influence of this gene was also bypassed by environmental factors. This hypothesis is strongly supported by the observations of sudden decline in marine growth rate and simultaneous increase in age at maturation in many Atlantic salmon populations inhabiting Northeast Atlantic rivers, presumably caused by the documented ecological regime shift in 2005 (Vollset et al., 2022). This region included the river Etne, where identical declines in growth rate and increase in age at maturation were observed (Harvey et al., 2022). However, whether the ecological regime shift in 2005 is the primary cause of the dissociation between genotype and sea age, or if it results from a longer process of declining marine growth conditions cannot be completely resolved here.

The novel observations reported here are associated with a single population. However, the existence of an extensive preaquaculture and pre-ecological regime shift set of historical samples, together with the upstream fish trap providing the systematic collection of accurate phenotypic measurements on the fish in recent years, has provided a unique and novel insight into the disassociation between *vgll3* and *six6* and age at maturation. At the same time, computation of admixture on representative samples of domesticated salmon captured in this river (Besnier et al., 2022), has provided the unique opportunity to exclude domestication driven admixture as the potential cause of these changes. As this (Harvey et al., 2022), and other salmon populations (Vollset et al., 2022) in the Northeast Atlantic were subjected to the same sets environmental changes, leading to consistently reduced marine growth rates and increased age at maturation, we believe that Etne is a representative example of many salmon populations in the same region, and conclude that growth-driven plasticity has almost completely bypassed the combined influence of *vgll3* and *six6* within on age at maturation, and furthermore, on resolving the sexual conflict for this trait in Atlantic salmon. While marine growth conditions may change from year to year, which may alter the relative influence of environmental versus genetic factors on this important life history trait from season to season, the principle of marine environmental conditions bypassing the importance of genetic factors on age of maturation have been documented in this study. Together with the interaction including sex-specific epistasis between *vgll3* and *six6* in the historical data, the dissociation between genes and age at maturation represents an original finding that changes our understanding of the genetic architecture of age at maturation in Atlantic salmon.

AUTHOR CONTRIBUTIONS

Øystein Skaala and Kevin A. Glover conceived and designed the study. Per T. Fjeldheim, Kaja Andersen-Fjeldheim and Øystein Skaala conducted the fieldwork and sample collection. Sofie Knutar conducted the laboratory work. François Besnier analysed and interpreted the data with critical input from Vidar Wennevik, Kjell Rong Utne and Kevin A. Glover. Fernando Ayllon, François Besnier and Kevin A. Glover led the writing with contributions from all coauthors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data for this study have been made available from the IMR.brage. unit.no public repository. This includes for all sampled individuals:

- Genotypes at all markers.
- Phenotypes (fish length, age at maturation and admixture estimate).

Link to data: https://imr.brage.unit.no/imr-xmlui/handle/11250/2987789.

BENEFIT-SHARING STATEMENT

The research addresses a priority concern regarding the consequences of climate change on salmonid populations in the North Atlantic. It was achieved thanks to the collaboration of the Etne river owners' association, and the results of the research were shared with collaborating partners in the form of annual open information meeting. In addition to the data supporting the present results and archived as described above, data generated from the fish trap in Etne are stored and freely accessible at the Norwegian Marine Data Centre.

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SUPPORTING INFORMATION

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

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