Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon

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Understanding the mechanisms by which populations adapt to their environments is a fundamental aim in biology. However, it remains challenging to identify the genetic basis of traits, provide evidence of genetic changes and quantify phenotypic responses. Age at maturity in Atlantic salmon represents an ideal trait to study contemporary adaptive evolution as it has been associated with a single locus in the vglL3 region and has also strongly changed in recent decades. Here, we provide an empirical example of contemporary adaptive evolution of a large-effect locus driving contrasting sex-specific evolutionary responses at the phenotypic level. We identified an 18% decrease in the vglL3 allele associated with late maturity in a large and diverse salmon population over 36 years, induced by sex-specific selection during sea migration. Those genetic changes resulted in a significant evolutionary response only in males, due to sex-specific dominance patterns and vglL3 allelic effects. The vglL3 allelic and dominance effects differed greatly in a second population and were likely to generate different selection and evolutionary patterns. Our study highlights the importance of knowledge of genetic architecture to better understand fitness trait evolution and phenotypic diversity. It also emphasizes the potential role of adaptive evolution in the trend towards earlier maturation observed in numerous Atlantic salmon populations worldwide.

A fundamental aim in biology is to better understand mechanisms underlying adaptation of populations to their environment14. Adaptation may represent the only way for certain populations to persist in the face of strong human pressures and accelerated rates of climate change altering their environment. Temporal monitoring has documented recent and rapid phenotypic changes in wild populations in many species (for example, refs 15–17). However, whether such phenotypic changes are adaptive, and the consequences of evolution and/or plasticity, often remain unclear18. Obtaining evidence of adaptive evolution requires knowledge of the genetic basis of traits and subsequent demonstration that natural selection induces changes in this genetic component. Although the ideal strategy for demonstrating adaptive evolution is to study the genes directly controlling the traits under selection, such examples are extremely scarce19. Despite the increased availability of genomic data, identifying large-effect loci controlling phenotypes of ecological significance, as well as how contemporary selection affects them, remains challenging. In cases where the genetic architecture of a trait is well characterized, it provides a rare opportunity to investigate the contemporary change in traits inferred from pure natural selection occurring at a large scale. We studied a 40-year time series of two closely related Atlantic salmon populations from Northern Europe with contrasting maturation age structure. Despite a low level of genetic divergence between them (FST = 0.012), one population (Tenojoki) displays a high level of life-history diversity, including a high proportion of large, later-maturing individuals in both sexes, whereas the other population (Inarijoki) consists primarily of individuals of younger maturation ages, and with less life-history variation, particularly in males13. Here, we used the 40-year time series to detect potential signs of adaptive evolution in age at maturity by contrasting allele frequency changes at the maturation-linked gene vglL3 with life-history phenotypes in 2,482 samples from the two populations. We also investigated the occurrence of sex- and population-specific genetic architecture and selection, potentially explaining the observed diversity variation in age at maturity.

Results

Temporal changes in age at maturity. We first quantified temporal phenotypic changes in both populations. There was a nonlinear decrease in the age at maturity of Tenojoki individuals, with the mean maturation age of males declining by >40% (from 2.2 to 1.3 years;
effective degrees of freedom (EDF) = 3.87, F = 5.11, P < 0.001) and that of females declining by 8.1% (from 3.0 to 2.7 years; EDF = 1.27, F = 0.57, P = 0.02) during the 36-year time period (Fig. 1a). In Tenojoki males, the decrease occurred primarily between 1971 and 1987 before stabilization, while in females, the age at maturity gradually decreased over the 36-year study period, explained best by a slightly nonlinear slope (Fig. 1a and Supplementary Information). In comparison, Inarijoki males were virtually devoid of variation in age at maturity, with almost all males having spent one year at sea before maturing (EDF = 0, F = 0.00, P = 0.731), whereas the mean age at maturity in females fluctuated cyclically over the 37 years (EDF = 10.14, F = 6.035, P < 0.001; Fig. 1b), but with no indication of a decrease in the average maturation age (Fig. 1b).

Genetic architecture of age at maturity. Hereafter, we use genetic architecture to refer to the additive and dominance effects of vgll3 on age at maturity. The vgll3 genotypes had a sex-specific effect on the probability of observing the different ages at maturity in the Tenojoki population (χ²(6) = 27.58, P < 0.001). A sex-specific dominance pattern was observed in this population; heterozygote males had a mean age at maturity closer to homozygotes with double the allele associated with early maturity (the EE genotype) (that is, the allele associated with late maturity (vgll3*L) was partially recessive; estimated male dominance hₘ = 0.09, 95% CI = 0.02 to 0.17; see Methods), whereas heterozygote females had a phenotype closer to homozygotes with double the allele associated with late maturity (the LL genotype) (that is, the vgll3*L allele was partially dominant, estimated female dominance hₐ = 0.80, 95% CI = 0.65 to 0.92; Fig. 2a). In the Inarijoki population, vgll3 genotypes were significantly associated with the probability of observing the different age at maturity groups (χ²(6) = 56.41, P < 0.001), but not in a sex-specific manner (χ²(8) = 8.27, P = 0.08; vgll3*L was partially recessive in Inarijoki males and females, hₘ = 0.13, 95% CI = 0.05 to 0.31; and hₐ = 0.32, 95% CI = 0.17 to 0.50). Differences in the mean age at maturity between homozygotes varied depending on the sex and population (that is, additive or allelic effects—effects of the substitution of one allele for the other). In the Tenojoki population, the relative difference in mean age at maturity between alternative vgll3 homozygotes was about three times higher in males (+106% for LL, +1.17 years, 95% CI = 0.99 to 1.33) than in females (+32% for LL, +0.71 years, 95% CI = 0.51 to 0.91). This pattern was inverted in the Inarijoki population, with the relative difference in mean age at maturity between female homozygotes being about six times larger (+74% for LL, +0.94 years, 95% CI = 0.68 to 1.25) than in males (+12% for LL, +0.13 years, 95% CI = 0.05 to 0.22; Fig. 2b). Given that survival at sea is dependent on migration duration, these results imply that selection during sea migration (that is, the relative difference in survival between genotypes) is likely to vary between sexes and populations. There was no statistically significant change in the effect size of vgll3 on maturation age over time in either population (Tenojoki: χ²(6) = 6.07, P = 0.42; Inarijoki: χ²(4) = 4.41, P = 0.35).

Evolution of vgll3 and signals of selection. The vgll3*L allele frequency decreased significantly from 0.66 to 0.54 (18%) in 36 years in the Tenojoki population (F₁ = 0.009; log-odd slope = −0.014, 95% CI = −0.004 to −0.024; Fig. 3a). This allele frequency change was the highest of the 144 genome-wide single-nucleotide polymorphisms (SNPs) assessed and could not be explained by drift alone (P₁ = 0.004; Fig. 3a), nor after accounting for sampling variance (P₁ = 0.022). This observation provides strong support for natural selection acting against the vgll3*L allele in the Tenojoki population (see Supplementary Information). In the Inarijoki population, the trend in the vgll3*L allele frequency was also negative (log-odd slope = −0.009, 95% CI = −0.023 to 0.006), but not significant (F₁ = 1.29, P = 0.26; Fig. 3b). About 10% of the 135 genome-wide SNPs assessed had a larger change in allele frequency than vgll3 in this population (Fig. 3b). Consequently, we could not rule out drift as the basis of this change (P₁ = 0.189 for drift; and P₁ = 0.292 after accounting for sampling variance).

To further quantify the strength of selection driving changes in vgll3 allele frequency, a Bayesian model was used to estimate selection coefficients while accounting for genetic drift, similar to a Wright–Fisher model (see Methods). The selection coefficient in favour of the vgll3*L allele had a larger effect size of −0.004 to 0.08; Fig. 4), but 53% lower in the Inarijoki population (95% CI = 0.40 to 0.65, F₁ = 36.51, P < 0.001; Fig. 4). This could be the result of either the sex- and genotype-specific fertilization ratio or juvenile mortality in freshwater, or alternatively, selection at the vgll3 locus differing between the sexes during sea migration, before they return to reproduce. To distinguish the latter possibility (selection at sea) from options involving selection during the freshwater phase, we genotyped 143 and 108 juveniles of various ages (1–3 years old; see Methods) collected from the same freshwater locations in Tenojoki and Inarijoki, respectively. Juvenile sex ratios were close to parity and the vgll3*L allele frequency was similar in both sexes in both populations (χ²(1) = 3.27, P = 0.07 in Tenojoki; and χ²(1) = 0.04,
We provide convincing evidence of rapid adaptive evolution of age at maturity when the proportion of heterozygotes is increasing. Most of the observed decline in female age at maturity could be explained by the spawning years (0.20 years, EDF = 50%, F = 3.95, P < 0.001). The years effect also explained a part of the decline in male age at maturity (0.15 years, EDF = 3.51, F = 3.95, P < 0.001). The years effect also explained a part of the decline in male age at maturity (0.15 years, EDF = 3.51, F = 3.95, P < 0.001). The years effect also explained a part of the decline in male age at maturity (0.15 years, EDF = 3.51, F = 3.95, P < 0.001).

**Discussion**

We provide convincing evidence of rapid adaptive evolution of age at maturity towards small, early-maturing individuals in a large Atlantic salmon population. This indicates that despite having a
reproductive advantage due to their large size\textsuperscript{12,19}, the late maturation life-history strategy has become increasingly costly and modified the reproductive success versus survival trade-off such that earlier maturation is increasingly advantageous. Adaptive evolution may thus represent a realistic mechanism behind changes towards earlier age at maturity observed worldwide in the past decades in Atlantic salmon (for example, refs \textsuperscript{14–16,20}) and other salmonid fish species (for example, ref. \textsuperscript{21}). What could be the causes of such rapid evolution of a life-history trait? One explanation is that it could be linked to recent rapid changes in the marine environment of the Teno salmon populations. For example, climate change may negatively affect Atlantic salmon marine growth and/or survival directly (for example, ref. \textsuperscript{21}) or indirectly through changes in Arctic food webs and ecosystem functioning resulting from, for example, species range expansions\textsuperscript{21,23,24}. Atlantic salmon occupying the northernmost parts of the globe will be unable to move to a colder climate in response to ocean warming, which would reinforce the importance of adaptation for population persistence. Another possibility is human-induced evolution of age at maturity through fishing targeting Atlantic salmon differentially according to their size, and therefore age at maturity (for example, ref. \textsuperscript{21}, but see ref. \textsuperscript{29}), or reducing prey abundance (for example, ref. \textsuperscript{21}). Such environmental changes and/or human-induced pressure could negatively affect salmon survival at sea and thus increase the cost of late maturation, thereby potentially tipping the selective balance such that the size advantage at reproduction stemming from spending additional years at sea no longer compensates for the increased mortality and thus drives evolution towards a younger maturation age. However, it is important to note that natural selection did not entirely explain the observed temporal changes in age at maturity in the Tenojoki population. Irrespective of the \textit{vgll3} genotypes, the probability of early maturation increased over time (Supplementary Information). This could be due to adaptive phenotypic plasticity\textsuperscript{21}, through changes in maturation probability in the same direction as selection, or due to changes in allele frequencies at additional loci with smaller effects. Further investigation is required to test these hypotheses. Regardless, such changes in population age structure can negatively affect the population growth rate and/or temporal stability induced via portfolio effects (for example, ref. \textsuperscript{20}) and also have negative consequences on genetic diversity levels (for example, ref. \textsuperscript{20}). Therefore, they are a concern for future population persistence.

Despite common temporal changes in the \textit{vgll3} allele frequency between the sexes, differing genetic architectures, in terms of additive and dominance patterns, contributed to sex-specific selection strengths and evolutionary responses to selection. We observed sex-specific differences in \textit{vgll3} allele frequencies in adult salmon that were not present in pre-marine-migration juveniles from the same populations (Fig. 4). Interestingly, the direction of the sex-specific differences was opposite in the two populations studied. The combined effects of sex-dependent dominance and sex-specific selection patterns can explain these contrasting patterns. Indeed, large between-population variation in \textit{vgll3} effects on age at maturity may influence selection and the adaptive responses of individuals. The relative strength of allelic effects differed dramatically between the sexes and these effects were in opposite directions in the two populations: in the Inarijoki population, the difference in mean age at maturity between homozygotes was about six times larger in females compared with males, whereas in the Tenojoki population, the relative difference was three times higher in males (Fig. 2). Therefore, selection against \textit{LL} genotype individuals acts primarily on females in the Inarijoki population, but on males in the Tenojoki population (Fig. 4 and Supplementary Information). However, sex-specific dominance also plays a role by introducing differences in allele frequencies between the sexes that are dependent on the population allele frequency (Supplementary Fig. 2). Furthermore, sex-specific genetic architectures induce sex-specific evolutionary responses in the Tenojoki population by accelerating the decrease in age at maturity in males and reducing the temporal phenotypic variation in females. Sex-specific dominance is likely to have evolved to reduce intralocus sexual conflict\textsuperscript{10}. However, whether this genetic architecture is presently at its optimum is questionable in light of the quick decrease in \textit{vgll3*L} allele frequency and age at maturity. Further studies are necessary to determine whether sexually antagonistic selection in the Tenojoki population is persisting in ever-changing environments, and to describe the extent, origin and consequences of among population variation in genetic architecture.

Age at maturity evolved rapidly under sex-specific selection in just 36 years, equivalent to 4 to 6 generations in Atlantic salmon. Despite being genetically similar, the two studied populations had distinctive genetic architectures, sex-specific selection and, consequently, \textit{vgll3} allele frequency variation. This study shows that variability in genetic architectures can create complex selection and
The most likely number of clusters determined with the ΔK method was two when juvenile and adult data were combined (Supplementary Fig. 6). Juveniles were assigned accordingly to their sampling location in more than 96% of cases (Supplementary Fig. 7). Using the juvenile data as a baseline, 90% of adults were classified to one of the two clusters with probabilities equal to or higher than 0.8. Individuals sampled in Tenojoki were assigned to the Inarijoki population in 25% of the cases, whereas only 2% of the individuals caught in Inarijoki were assigned to the Tenojoki population. In total, 1,330 and 911 individuals clustered in the Tenojoki and Inarijoki populations, respectively (Supplementary Fig. 9). The two populations were significantly genetically differentiated (FST = 0.013, G = 201.55, P < 0.001) and had contrasted age structures (Supplementary Fig. 9).

Statistical analyses. Temporal variation in age at maturity and proportion of females. Nonlinear temporal variation in age at maturity was estimated separately for each population using additive models, with a random effect of local adaptation family and including the year of hatching as independent variables in the residual distribution. Year of hatching was included as an independent variable inside a cubic regression spline for each sex. The study included spawning individuals caught over a 43-year period (1972 to 2014). Hatch years were calculated based on the specific life-history strategy of each individual and spanned the period from 1971 to 2006 in Tenojoki and 1971 to 2007 in Inarijoki. Sex was also included as an explanatory variable.

The amount of smoothing was determined in each case using the maximum likelihood method. Automatic smoothness selection was performed by adding a shrinkage term. The significance of independent variables was assessed using F-tests and an alpha risk of 0.05. All statistical tests included in this manuscript were two-tailed. The additive models were run with the R package mgcv.

Effect size of vgll3 on age at maturity. To estimate the genetic effect of vgll3, age at maturity was also regressed using a multinomial model separately for each population. In Tenojoki, two individuals having matured after five years at sea were considered, as they had matured after four years to avoid over-parametrizing the model parameters without data support. Sex, year of capture and vgll3 genotype can influence age at maturity and were included in models as a three-way interaction. Multinomial models in this study were performed using the R package nnet. Model selection was performed using backward selection with F-tests, and by calculating the corrected Akaike’s information criterion of all possible models. The effect of year on the probability of maturing was calculated with the Effect package, which averages the effect size across sexes and genotypes. The mean age at maturity per sex and genotype was calculated from model-predicted values. First, predicted age was obtained for each year, sex and age at maturity combination by multiplying the probabilities of having any of the number of years spent in the marine environment before maturation (sea age) and possible previous spawning events, following international guidelines. The Teno river Atlantic salmon have diverse life-history strategies. They can spend from one to eight years in freshwater before smolting/frying, from one to five years at sea before maturing, and have up to five breeding attempts. Overall, a total of 120 combinations of river age, sea age at maturity and repeat spawning strategies have been described. Age at maturity has been declining in Teno salmon over the past 40 years, with proportionally fewer late-maturing salmon returning over the years. Age at maturity also differs largely among populations displaying genomic signatures of local adaptation.

We randomly selected samples from individuals caught by rod between 1972 and 2014 during the latter part of the fishing season, from 20 July to 31 August. Most of the Teno salmon are expected to have reached their home river by late July. Samples came from two different locations: the middle reaches of the Tenojoki mainstem (hereafter Tenojoki) and a headwater region, Inarijoki (Supplementary Fig. 5). These sections of the river host weakly differentiated salmon populations with contrasting sea-age structure at maturity. Individuals from the Tenojoki population spend, on average, more time at sea before maturing than individuals from the Inarijoki population. Seventy additional females were selected in Inarijoki over the study period, by following the same sampling scheme, to increase the sampling size in analyses with sex-specific estimates. Scale or fin samples were also collected from juvenile salmon from the Tenojoki (n = 143, 2–3 years old) and Inarijoki (n = 108, 1–3 years old) populations caught by electrofishing in 2014–2015 and 2016, respectively. These were used as the baseline for population assignment of adults, and to determine potential sex-specific vgll3 allele frequency differences at the juvenile stage. Fishing permission for research purposes was granted by the Lapland Centre for Economic Development, Transport and the Environment (permit numbers 1579/5713–2007 and 2370/5713–2012).

Genotyping. DNA extraction from scales, sex determination and genotyping were performed following ref. 10. In total, 2,482 individuals were genotyped at 191 SNPs, including the SNP most highly associated with age at maturity, vgll3TOP (a vestigial-like family member 3 gene, also called vgll3), and outlier and baseline SNP modules. The outlier module consisted of 53 SNPs highly differentiated between the Tenojoki and Inarijoki populations, thus allowing a more powerful assignment of the population of origin between these two closely related populations (see refs 8,10). The baseline module included 136 putatively neutral markers in local linkage disequilibrium, distributed over the whole genome proportional to chromosome length, previously filtered to have a minor allele frequency of >0.05 and heterozygosity of >0.2 (ref. 10). Those SNPs were used to estimate the level of differentiation among populations of the Teno River (Weir and Cockier model FST/θ pattern), 143, 2–3 years old) and h = 0.5 and dominant if h = 1.

To determine what proportion of the observed changes in age at maturity over time could be attributed to changes in genotypes and year of capture, a new dataset with the spawning year held constant at 1975 was created for Tenojoki. The previous multimodal model was used to predict new maturation probabilities from which the model-predicted age at maturity was calculated for each individual, as described above. Temporal changes in age at maturity attributed to genotypes were determined by fitting a generalized additive model using the Gaussian family and including the individual hatch year in a cubic regression spline and the sex as an independent variable. Changes in age at maturity attributed to the year of capture corresponded to the difference between the individual predicted age at maturity calculated from the original dataset and the one with the year fixed. Another Gaussian generalized additive model was also performed on those differences, including by the hatch year in a cubic regression spline. Automatic smoothness selection was performed by adding a shrinkage term.

Change in allele and genotype frequencies. Temporal variation in allele frequencies was determined for each population and locus using generalized linear models (GLMs), with the quasibinomial family to account for overdispersion. Sex-dependent vgll3 genetic effects on the age at maturity may create sex-specific selection at sea, leading to differences in the vgll3 allele frequency between male and female spawners from different populations. To capture this potential intragenration variation in allele frequency, hence, sex and year of hatching were included as independent variables in the GLM. To keep the potential effect of sex-specific selection on the vgll3 allele frequency temporal change, the model was also run without including sex as a covariate. The significance of variables was assessed using F-tests.

To determine whether the vgll3 allele frequencies varied across time more than under the neutral expectation, model-predicted temporal changes in allele frequencies were compared among loci with individual genotyping success higher
than 0.7 (144 and 135 loci for the Tenojoki and Inarijoki populations, respectively). This threshold was chosen as a trade-off between increasing the quality and amount of data per locus (average genotyping success superior to 0.90 in those subsets) and keeping a large number of loci for the comparison (25–30% of loci were excluded). The amount of genetic drift, and thus random temporal allele frequency change, is dependent on the initial allele frequency of each locus

The comparison of temporal changes between vgl3 and other putatively neutral loci was thus corrected for initial allele frequency by calculating the expected amount of drift at vgl3 under a Wright–Fisher model.

The distribution of allele frequency \( x(t) \) after \( t \) generations can be approximated using a normal distribution:

\[
\begin{align*}
    x(t) & \sim \text{Normal} \left( x(0), \sigma^2 \right), \\
    \sigma^2 &= \frac{\sigma_0^2}{2N},
\end{align*}
\]

with \( x(0) \) being the initial allele frequency and \( N \) the effective population size. The ratio \( \frac{\sigma^2}{\sigma_0^2} \) was estimated with a Bayesian model using a uniform prior distribution ranging from 0 to 1. The binomial fitted allele frequencies at hatching for the years 1971 (\( x(0) \)) and 2006 (\( x(t) \)) in Tenojoki and 1971 (\( x(0) \)) and 2007 (\( x(t) \)) in Inarijoki were used as data for all loci except vgl3. Two MCMC chains were run for 200,000 iterations with a thinning interval of 10, including a burn-in length of 100,000. Convergence was assessed using the Gelman and Rubin’s convergence diagnostic and a potential scale reduction factor (PSRF) threshold of 1.1. The probability of observing the vgl3 allele frequency change (\( \Delta_{\text{vgl3}} = x(t) - x(0) \)) under drift alone was calculated at each of the 20,000 saved iterations \( i \) to account for uncertainty in the \( \xi \) estimation as follows:

\[
P_{\Delta_{\text{vgl3}}} = 1 - \frac{1}{20,000} \sum_{i=1}^{20,000} \left| \Delta_{\text{vgl3}}^i - \Delta_{\text{vgl3}} \right|
\]

with \( \Delta_{\text{vgl3}} = x(t) - x(0) \).

To account for further uncertainty in the vgl3 allele frequency change, \( \Delta_{\text{vgl3}} \) was re-estimated at each iteration \( i \) by running the quasibinomial model with a new dataset, sampled for each year from the original dataset with replacement. The distribution of changes expected under drift alone was also calculated in the same manner as for vgl3, for initial allele frequencies \( x(0) \) varying from 0.5 to 1.

To determine whether potential differences in vgl3 allele frequencies between adult males and females are likely to arise during the sea migration, juvenile allele frequencies were analysed using a separate GLM with the binomial family for each population. Sex was introduced as an independent variable. A backward model selection was performed using likelihood-ratio tests and an alpha risk of 0.05. CIs were calculated with the lme4 package by taking the years 2006 and 2007 as reference for the Tenojoki and Inarijoki adults, respectively.

Allele frequencies may differ between the sexes due to sex-specific selection between homoygotes, but also because of the effect of sex-specific dominance, even when selection is sex independent. To determine how dominance can contribute to differences in allele frequencies between the sexes, the expected sign and magnitude of allele frequency differences were determined for different selection strengths, using the dominance patterns calculated previously for the Inarijoki and Tenojoki populations. Considering a gene with two alleles, \( A \) and \( B \), with respective frequencies \( p \) and \( q \), the allele frequency after a selection event corresponds to:

\[
P_i = p_i^2 \text{W}_{AA} + p_i q_i \text{W}_{AB} + p_i q_i \text{W}_{BB}
\]

with \( \text{W}_{AA}, \text{W}_{AB}, \) and \( \text{W}_{BB} \) the relative fitness of each respective genotype:

\[
\text{W}_{AA} = 1; \quad \text{W}_{AB} = 1-\text{DS} \quad \text{and} \quad \text{W}_{BB} = 1-S
\]

where \( S \) is the selection coefficient common to each sex, varying from 0 to 0.90 by 0.15 intervals, and \( D \) is the dominance coefficient. \( p_i \) was calculated for each sex and population using the corresponding dominance coefficients previously calculated from phenotypes (\( D = h \)) and an initial \( p \) varying from 0 to 1. The expected difference in allele frequency in Supplementary Fig. 2 corresponds to \( p_i \) (female) – \( p_i \) (male), calculated for each combination of \( S \) and \( p \).

First, the linkage disequilibrium method implemented in the software NeEstimator 2.01 (ref. 77) was applied on samples grouped by cohort year to estimate the parental effective number of breeders (\( N_e \)). This approach was favoured over the standard temporal method potentially generating biased effective size estimates when used with temporally close samples from species with overlapping generations and only providing information about the harmonic mean of effective sizes. To use the linkage disequilibrium \( N_e \) values and associated 95% posterior CIs in the Bayesian models, parameters of log-normal distributions with similar percentiles were assessed using the R package riskDistributions.

Weights of 7.2 and 1 were assigned, respectively, to the 2.5, 5.0 and 97.5 percentiles to increase the approximation precision for lower bounds and medians. The negative or infinite values were replaced by 5,000 or 10,000 for the median and 95% CI upper bound, respectively. These are realistic maximum breeder numbers in the populations and represent a conservative approach. If the lower bound also displayed infinite values, the corresponding distribution had a median of 9,000, and lower and upper bounds of 8,000 and 10,000, respectively.

The selection coefficient represents “the reduction in relative fitness, and therefore genetic contribution to future generations, of one genotype compared to another”.

Selection coefficients were estimated using 32 and 33 different spawning years, with corresponding hatch years, for Tenojoki and Inarijoki, respectively. Considering a SNP with alleles 1 and 2, \( W^{11} = 1, W^{12} = 1-\text{DS} \) and \( W^{22} = 1-S \) representing the relative fitness of each genotype. \( S \) corresponds to the selection coefficient, following a uniform prior distribution ranging from 1 to 1, and \( D \) denotes the dominance coefficient, following a uniform prior distribution ranging from 0 to 1. The observed number of each genotype \( g \) in spawners of sex \( s \) in year \( (t, y) \) followed a Dirichlet multinomial (DM) distribution:

\[
N_g = \text{DM}(T_y, g^{11}, g^{12}, g^{22}, \eta),
\]

where \( \eta \) is the variation parameter following a uniform distribution ranging from 1 to 2,500 and \( T_y \) is the total number of spawners per sex and year.

The spawners genotype frequency for each sex \( g = (g^{11}, g^{12}, g^{22}) \) varied over years according to a hierarchical model, \( g^{11} \sim g^{12} \sim g^{22} \sim \text{Dirichlet}(\mu^{11}, \mu^{12}, \mu^{22}) \) and \( \mu^{11} = \mu^{12} = \mu^{22} \) – Dirichlet(1, 1). The observed number \( A \) of alleles \( n_j \) in individuals born in year \( y \) follow a binomial distribution:

\[
n_j = \text{Binomial}(p_j, 2N_s),
\]

where \( N_s \) is the total number of individuals per year and \( p_j \) is the population allele frequency. The expected allele frequency in the cohort \( y \) depends on the genotype frequency in spawners the year before, as follows:

\[
E(p_j) = \frac{n_j^{11} W^{11} + 0.5 n_j^{12} W^{12} + n_j^{22} W^{22}}{N_s}.
\]

with \( W^{11} \) being the population mean fitness \( W = s_{11} W^{11} + s_{12} W^{12} + s_{22} W^{22} \), \( s_{11}, s_{12}, s_{22} \) are the genotypes of spawners averaged across sexes, and each sex contributes equally to the next generation despite a potential biased sex ratio.

Genetic drift should be taken into account to estimate \( p_j \) from the genotype frequencies of the previous year’s spawners. In populations with random mating, it corresponds to drawing \( p_j \) randomly from a binomial distribution with as parameters, the expected allele frequency \( E(p_j) \) and twice the effective number of spawners, previously estimated by the linkage disequilibrium method (\( 2N_e \)).

Consequently, the expected variance of the allele frequency \( p_j \) subject to drift is after one generation \( \text{Var}(p_j) = \frac{2N_e}{N_s} \).

For computing time and convergence reasons, a beta distribution with equal mean and variance was used instead:

\[
p_j = \text{Beta}(\alpha, \beta).
\]

with

\[
\alpha = \frac{E(p_j) \text{Var}(p_j) + E(p_j^2) - E(p_j^2)}{\text{Var}(p_j) - (E(p_j^2) - E(p_j)^2)}, \quad \beta = \frac{E(p_j) \text{Var}(p_j) + E(p_j^2) - E(p_j)^2}{\text{Var}(p_j) - (E(p_j^2) - E(p_j)^2)} - 1.
\]

Priors used in this model were chosen to be as uninformative as possible. A surrogate for \( \alpha \) value named ‘pPMC’ was calculated for the selection coefficient \( S \) from the two chains as follows: \( \alpha = \text{mean} (pr (S < 0); 1 - pr (S < 0)) \), \( pr (S < 0) \) is the proportion of \( S \) values below zero.

Posterior distributions were approximated using MCMC methods with the JAGS \(^{84} \) run in the R environment. Two MCMC chains were run for 4.5 million iterations, including a burn-in length of 3.5 million. Only 1 iteration out of 100 was kept to reduce the memory size used. Gelman and Rubin’s convergence diagnostic \(^{85} \) was used to assess convergence. Models were run longer than the PSRF was initially superior to 1.10. Finally, all models had a PSRF inferior or equal to 1.10 for all parameters, except for up to 2 \( N_e \) parameters in 10 models for Inarijoki, having larger PSRF (inferior to 1.30).
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Author contributions
J.E. and P.O. coordinated the collection of samples. C.R.P., Y.C., T.A. and J.E. designed the study. Y.C. analysed the data. Y.C., C.R.P. and T.A. wrote the manuscript. All authors contributed to revision of the manuscript.

Competing interests
The authors declare no competing interests.

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Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection  
Aykanat et al. 2016 for genotyping

Data analysis  
R statistical software 3.4.0 (packages mgcv, Effect, lsmear, rriskDistributions, nnet, rjags, coda), JAGS 4.2.0, STRUCTURE 2.3.4, STRUCTURE HARVESTER 0.6.94, CLUMP 1.1.2, NeEstimator 2.01

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The data supporting the findings of this study are available in the Dryad Digital Repository with the identifier doi:10.5061/dryad.7hm4708.
Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description: Temporal changes in age at maturity and vgll3 allele frequency in Atlantic salmon. Data is quantitative (number of alleles, age at maturity) and qualitative (sex).

Research sample: Scales from Atlantic salmon caught with a single gear (rod) to avoid differences in size selection over time. Those samples should be representative of the population.

Sampling strategy: Random sampling from 1972 to 2014, 2482 adult individuals caught by rod, from two populations. The objective was to obtain on average, after population assignment, 50 individuals per years (here 54), considered sufficient for the type of analyses performed. Juveniles were sampled by electrofishing in 2 locations (several hundred metre stretches in both locations to minimise the chance of sampling siblings).

Data collection: The LUKE institute collected the samples provided by fishers and saved associated information in excel sheets.

Timing and spatial scale: 2 different locations, sampling of adults returning from migration each year from 1972 to 2014, except in 1973 and 1974.

Data exclusions: Individuals not genetically assigned to Tenojoki or Inarijoki with probabilities higher than 0.8 were excluded from the data. Only high quality SNPs with genotyping success higher than 0.7 were included for trends comparison with the vgll3 SNP and selection estimates. Sixty seven additional females were randomly sampled in Inarijoki to partially compensate the highly biased sex-ratio and were included only in analyses with sex-specific parameters.

Reproducibility: There is no experimentation in this study.

Randomization: There is no experimentation in this study.

Blinding: There is no experimentation in this study.

Field work, collection and transport

Field conditions: The field study took place in the Teno river and were subjected to normal field conditions in this area at this time https://www.yr.no/place/Finland/Laponia/Utsjoki/statistics.html

Location: Electrofished individuals were from Teno River, near the mouth of the Utsjoki tributary (69°54'28.37''N, 27°2'47.52''E) and Inarijoki river (69°35'5.82''N, 25°57'46.73''E), Finland. Water depth at sampling was approximately 1m.

Access and import/export: Fishing permission for research purposes was granted by the Lapland Centre for Economic Development, Transport, and the Environment (permit numbers 1579/5713-2007 and 2370/5713-2012).

Disturbance: Care was taken to minimize disturbance to the areas by handling the fish as quickly as possible.

Reporting for specific materials, systems and methods
Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

| Laboratory animals | This study did not involve laboratory animals |
|--------------------|---------------------------------------------|
| Wild animals        | Atlantic salmon scales were collected by fishers (rod catches, males and females of varying ages). Juvenile samples were collected by electrofishing by trained researchers. |
| Field-collected samples | Scales samples were stored in envelops, at room temperature. Fin clips from electrofished juveniles were stored in 95% ethanol. |