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## Rapid evolution in salmon life history induced by direct and indirect effects of fishing

Czorlich, Yann

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**Title: Rapid evolution in salmon life-history induced by direct and indirect effects of fishing**

**Authors:** Y. Czorlich<sup>1,2,3,4</sup>, T. Aykanat<sup>3</sup>, J. Erkinaro<sup>2</sup>, P. Orell<sup>2</sup>, & CR. Primmer<sup>3,5\*</sup>

5 **Affiliations:**

<sup>1</sup> University of Turku, Department of Biology, FI-20014, Turku, Finland.

<sup>2</sup> Natural Resources Institute Finland (Luke), POB 413, FI-90014 Oulu, Finland.

<sup>3</sup> University of Helsinki, Organismal & Evolutionary Biology Research Programme, POB 56, FI-00014 Helsinki, Finland.

10 <sup>4</sup> Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway.

<sup>5</sup> University of Helsinki, Institute of Biotechnology, Helsinki Institute of Life Science (HiLIFE), POB 56, FI-00014 Helsinki, Finland.

[\\*craig.primmer@helsinki.fi](mailto:craig.primmer@helsinki.fi)

15 **One Sentence Summary:** Rapid evolution of age at maturity in salmon induced indirectly by prey harvest and directly via size-selective harvest.

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**Abstract:**

Understanding the drivers of evolution is a fundamental aim in biology. However, identifying the evolutionary impacts of human activities is challenging because of lack of temporal data and limited knowledge of the genetic basis of most traits. Here, we identify the drivers of evolution towards earlier age at maturity in Atlantic salmon via two types of fisheries-induced evolution acting in opposing directions: an indirect effect linked with harvest of a salmon prey species (capelin) at sea (selection against late maturation), and a direct effect due to net-fishing in the river (selection against early maturation). As capelin are harvested as an aquaculture feed protein source, we hereby determine an indirect path by which salmon aquaculture may influence wild salmon populations.

**Main Text:**

Indirect ecological effects, for example when a third species mediates the impact of one species on another (1), and their evolutionary impacts have often been neglected in studies of natural populations. For instance, fishing can induce evolution of traits such as size and age at maturity in the target species (2, 3) but also induce larger, ecosystem level, changes, some of which may be indirect. However, cases demonstrating direct effects at the genetic level are rare, as are empirical examples of indirect evolutionary impacts of fishing (2, 4). Knowledge of indirect ecological and evolutionary effects is critical for properly evaluating the consequences of different fisheries management strategies (5).

Atlantic salmon (*Salmo salar*) have a complex life-history, utilizing both freshwater and marine habitats and thus affect, and are affected by, multiple ecosystems (6). Sea-age at maturity in

Atlantic salmon (the number of years an individual spends in the marine environment before returning to fresh water to spawn), or sea age, is an important life history trait, that exhibits an evolutionary trade-off between survival and reproduction. Later maturing individuals are larger and have higher reproductive success (7) but run higher risk of mortality before spawning. Age at maturity has been associated with a major effect locus in the genome region including the *vgll3* gene that explains 40% of the variation in the trait (8). Adaptive evolution towards younger age at maturity at the *vgll3* locus over 40 years has earlier been demonstrated in a large Atlantic salmon population from the Teno river (Deatnu in Sámi, Tana in Norwegian) in northern Europe (9), but the environmental drivers of the evolution in age at maturity remained unknown.

Here, we investigate ecological and environmental variables potentially affecting the relative fitness of salmon with different maturation ages, and therefore sizes, from the same river: fishing effort at sea, fishing effort in the river, sea temperature, and the average biomass of three key prey species available during the years each salmon spent in the Barents Sea ecosystem (capelin *Mallotus villosus*, herring *Clupea harengus* and krill, fig. S1). We used individual-based (quasi)binomial generalized linear models (GLM) to identify environmental variables linked with temporal variation in *vgll3* allele frequencies (e.g. 10), and thereby age at maturity, in a 40 year time series (1975 – 2014) consisting of 1319 individuals genetically assigned to the Tenojoki population (hereafter Teno) in the middle reaches of the mainstem of the river system (9). These analyses indicate that annual number of riverine net-fishing licenses (a proxy for annual fishing pressure) had the strongest effect on *vgll3* allele frequency (Fig. 1). Surprisingly, annual riverine fishing pressure was positively associated with the *vgll3*\*L allele frequency (standardized regression coefficient  $\hat{\beta}^* = 0.42$ ,  $F(1) = 27.79$  and  $P\text{-value} < 0.001$ ) indicating that higher net-

fishing pressure in the river was associated with higher frequencies of the allele associated with later maturation in salmon and therefore larger size (table S1). We verified the results by de-trending the data (using a residual regression approach) to account for potentially confounding factors creating temporal trends between the dependent and independent variables, and thus avoid possible spurious associations (11). The association between annual net-fishing license number and *vgll3* remained in the de-trended model including a significant, negative, year effect, indicating that fishing pressure is also linked with annual *vgll3* allele frequency changes around the trend ( $\hat{\beta}^* = 0.17$ ,  $F(1) = 14.15$  and  $P\text{-value} < 0.001$ , Fig. 1, table S1). Capelin biomass in the Barents Sea was also positively associated with the frequency of the *vgll3* allele associated with later maturation and larger size (*vgll3*\**L*) in salmon in both the normal ( $\hat{\beta}^* = 0.23$ ,  $F(1) = 20.77$  and  $P\text{-value} < 0.001$ ) and de-trended models ( $\hat{\beta}^* = 0.14$ ,  $F(1) = 10.64$  and  $P\text{-value} = 0.001$ , table S1). Herring and krill biomass also had a significant effect on *vgll3* allele frequencies in a similar direction to capelin (Fig. 1, table S1), however, they did not remain significant in the de-trended model. There was little evidence for associations between the other variables and *vgll3* in the GLM (rod fishing licenses in the river, Barents Sea temperature, and net-fishing at sea; table S1).

Analyses at the phenotypic level indirectly support the influence of prey biomass and fishing on Teno salmon fitness. After controlling for the *vgll3* sex-specific genetic effects, a multinomial model indicates that the proportion of older, later maturing Atlantic salmon in the river increases with capelin, herring and krill biomass (table S2). This result is expected if the abundance of these prey species is positively associated with salmon survival at sea, as only survivors returning back to the river are sampled. However, it can also reflect plastic changes of maturation probabilities. This model also shows that a higher number of riverine net-fishing licenses associates with a higher

proportion of late maturing salmon being observed at the end of the fishing season (table S2), which is expected if net-fishing targeted preferentially small, early maturing salmon. Given that the sea-age at maturity of Teno females is, on average, considerably higher than males, and therefore the time spent in the marine environment longer (2.8 vs 1.5 years), environmental conditions strongly affecting marine survival are also expected to influence the sex-ratio of adults returning from their migration to spawn. In accordance with this prediction, a binomial model showed that the proportion of returning females increased with prey biomass and riverine net-fishing (fig. S2, table S3). The effects of riverine net-fishing on sex-ratio and age at maturity probability, however, were not significant in the de-trended regressions (table S2, table S3).

Forage fishes like capelin have important roles in marine ecosystems by enabling energy transfer between lower (plankton) and upper (predators such as large fish, seabirds and mammals) trophic levels (12). In the Barents Sea, the capelin stock experienced several dramatic collapses during the 40-year study period (fig. S3) due to overexploitation in commercial fisheries combined with predation by herring and cod (fig. S4, (13)). We therefore quantified the potential indirect effects of capelin harvesting (while accounting for other ecosystem interactions) on *vgll3* allele frequency dynamics using a multispecies Gompertz model developed in (14) (fig. S1, fig. S3, fig. S4). The analysis indicated a significant indirect effect of capelin harvest rate on age at maturity evolution in Teno salmon, with a 30% decrease in the *vgll3*\**L* allele odds per harvest rate unit (Monte Carlo method for assessing mediation: CI95% = [0.116, 0.471]). The evolutionary effect of capelin harvest was the strongest during the early years of the time series, likely because of repeated capelin fisheries closures and fishing effort reduction later on, following the capelin stock collapses (Fig. 2; fig. S5A). This is the same time period when most of the evolutionary changes

in male age at maturity occurred (9). However, by reducing the *vgll3\*L* allele frequency in adults that return to reproduce, the indirect fishing effect (Fig. 2) is also expected to impact the allele frequency of offspring in the next generation due to the lower *vgll3\*L* allele frequency in the breeders.

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The direction of the selection pressure in the riverine net-fishery may seem counter-intuitive as generally, net-fishing is thought to select against large individuals (e.g. 15, 16). However, net-fishing in the Teno river includes the use of multiple net types with different selectivity: weir, gillnet and driftnet (17). To estimate the size selectivity of different fishing gear types, we compared the size distribution of salmon caught with each fishing gear type during the fishing period in June and July to the size distribution of ascending salmon obtained from a sonar count in the river during the same period. This analysis indicates that weir fishing selects against the early maturation allele (*vgll3\*E*) by capturing a higher proportion of smaller, and earlier maturing, individuals whereas driftnet and gillnet select against the *vgll3\*L* allele (fig. S6, fig. S7).

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Discussions with indigenous Sámi fishers with decades of net-fishing experience indicated that the tendency for weirs to preferentially capture younger, smaller individuals could potentially arise from several factors, including the positioning of weirs mostly in shallower waters, their smaller mesh size and/or the timing of their use during the fishing season (Aslak Holmberg & Nils Antti Holmberg, pers. comm.). The positive effect of riverine net license number (including all net types) on the *vgll3\*L* allele frequency may thus be explained by the predominant use of weirs, the most selective fishing method (representing 54% of net catches on average). Over the time series, net-fishing effort declined dramatically due to stricter fishing regulations as well as a decrease in the number of indigenous fishers using weirs (for example, both net-fishing licenses and number of

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weirs were >30% lower in 2014 vs. 1976, fig. S5B). In addition to a decline in net-fishing effort, temporal changes in other factors may have resulted in a decrease in the size selectivity of net-fishing, including changes in the relative use of the different fishing gears as well as changes in salmon size distribution and sex-ratio (Fig. 3). As a consequence, the net-fishing selective pressure against the *vgll3\*E* allele is expected to have declined during the time series, which has likely resulted in improved riverine survival of early maturing salmon relative to older individuals. Overall, the extra mortality of late maturing *vgll3\*L* individuals at sea was not sufficiently compensated by their size-induced survival advantage due to riverine net-fishing (decreasing over time), nor their reproductive advantage due to larger size (7), thus resulting in an overall fitness loss and leading to the observed overall decrease in the *vgll3\*L* allele frequency (Fig. 2).

Using an ecosystem-level approach, we provide an example where both direct and indirect fishing effects have contributed to fisheries-induced evolution. Minimizing fisheries-induced evolution is generally recommended as adaptation of populations to fishing can hinder adaptation to their natural environment and be costly in the long run (18–20). However, strong socio-economic issues may limit opportunities for dramatic changes in fishing regulations to alter harvest rates to minimize fisheries-induced evolution (20). In the Teno river valley for instance, salmon fishing is both a key source of income for locals through fishing tourism, as well as the foundation of the indigenous Sámi culture and identity, and restrictive fisheries regulations can be controversial (21).

The varying selectivity of different net types may provide a means to manage the selection pressures exerted by fishing on the different ages at maturity and genotypes, for example, by regulating the relative use of the different fishing gears. Collection of additional data such as additional years of genetic stock assignment and sonar counting, and the development of models



coupling population dynamics and evolutionary genetics would be required prior to implementation. Such models would also help in identifying selection driven by factors such as fishing at a constant harvest rate that could not be detected using regressions and in determining the impact of fisheries-induced selection on population growth rate. Commercial harvesting of an important salmon prey species, capelin, appears to have indirectly induced evolution of Atlantic salmon age at maturity toward younger, smaller individuals. Several studies have noted the potential for a fishery to induce ecological effects beyond the target species (22). However, evolutionary effects have not been demonstrated earlier (2, 4). Our study also has important implications of a more applied nature. About 90% of the forage fish catch are used for fish oil and fishmeal to feed farmed animals (12) and salmonid fish aquaculture is the 4th highest consumer (23). For instance in 2012, 75,800 tons of capelin was used in Norwegian aquaculture salmon feed (representing 15% of the marine ingredients (24)). Our results therefore identify a new indirect path by which Atlantic salmon aquaculture can affect wild populations of the same species and emphasize the importance of identifying alternative, sustainable, protein sources for the aquaculture industry.

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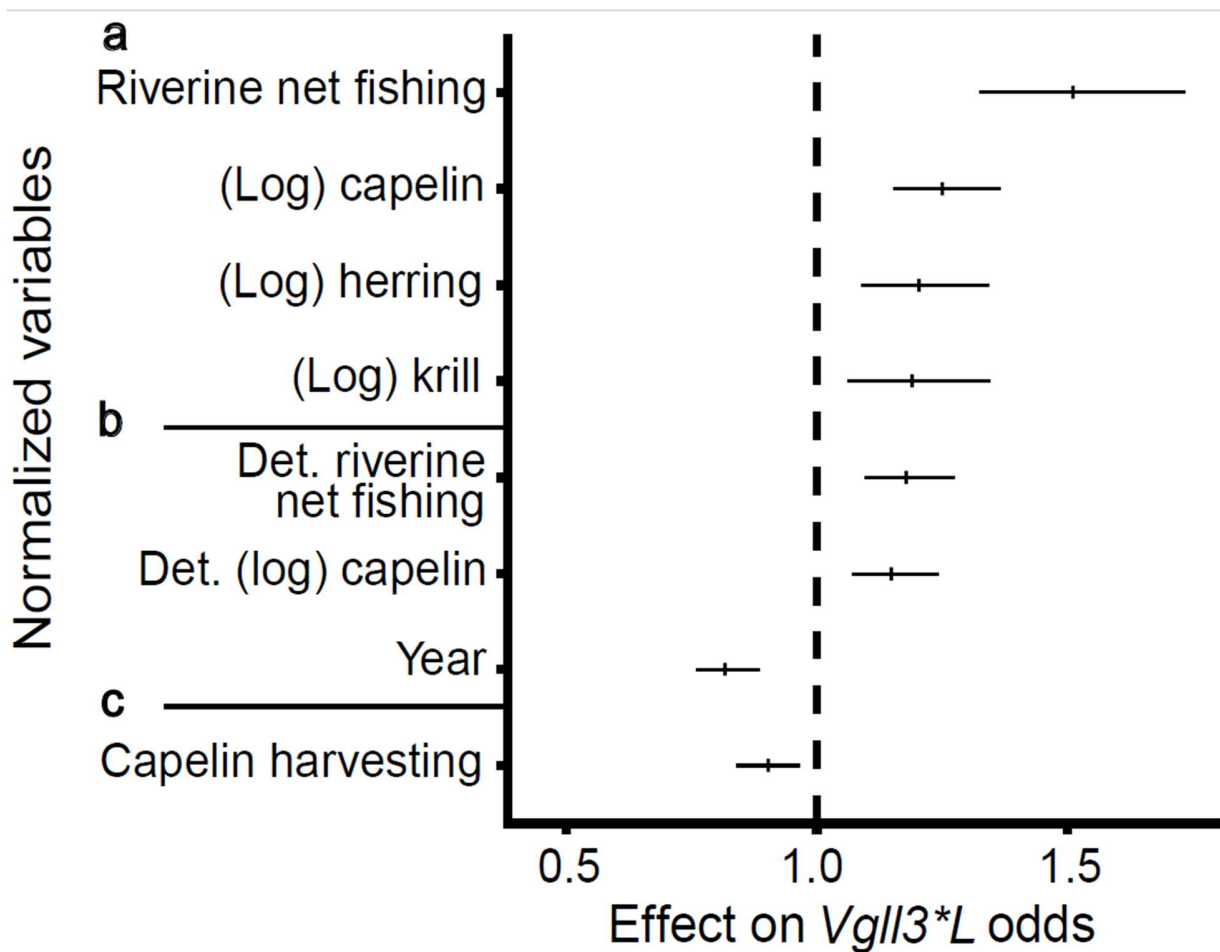
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**List of Supplementary Materials:** The Supplementary Materials include the Materials and Methods, and Supplementary figures S1-8 and tables S1-4. References 25-59 are only cited in the Supplementary Materials.

5 **Figures**

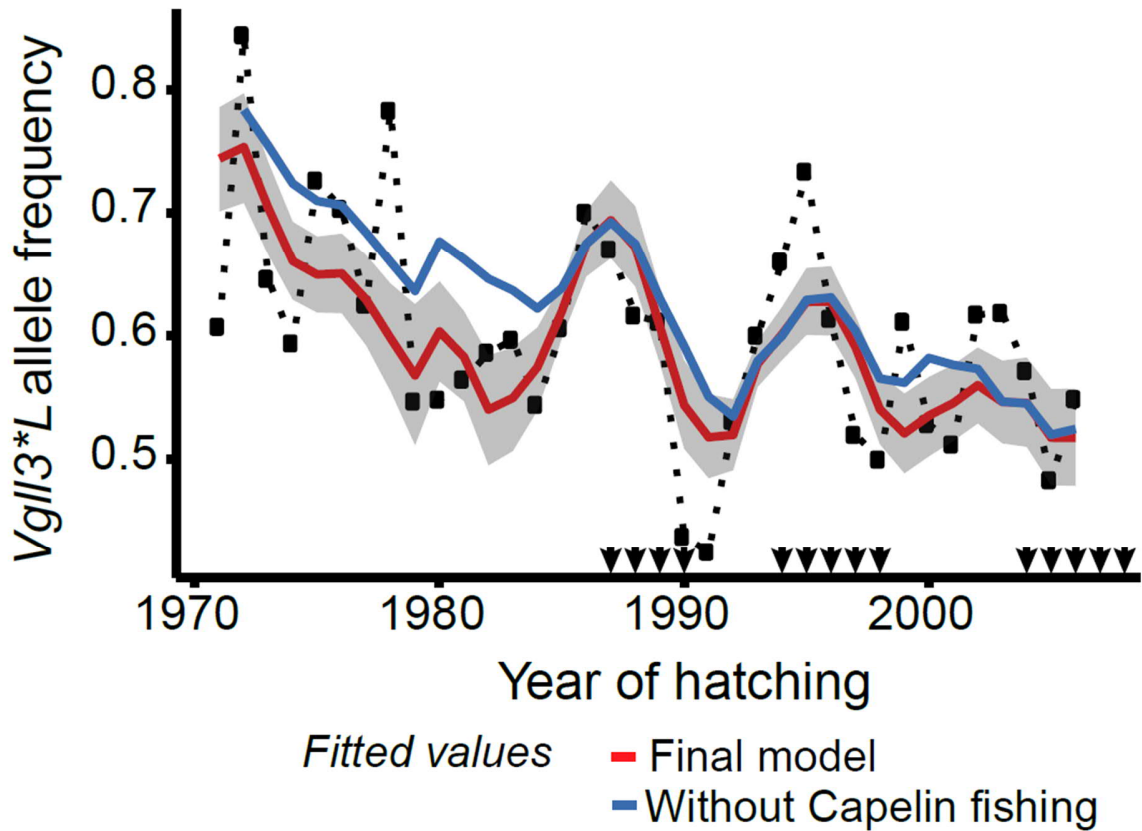


**Fig. 1. Standardized regression coefficients for variables significantly associated with *vgll3*\**L* odds (later, larger, maturation).** The estimates come from the a) initial quasi-binomial model. b) de-trended model. c) Monte Carlo Method for assessing mediation (i.e. indirect effects). The dotted line indicates no effect on *vgll3*\**L* odds. The error bars correspond to 95% confidence intervals.

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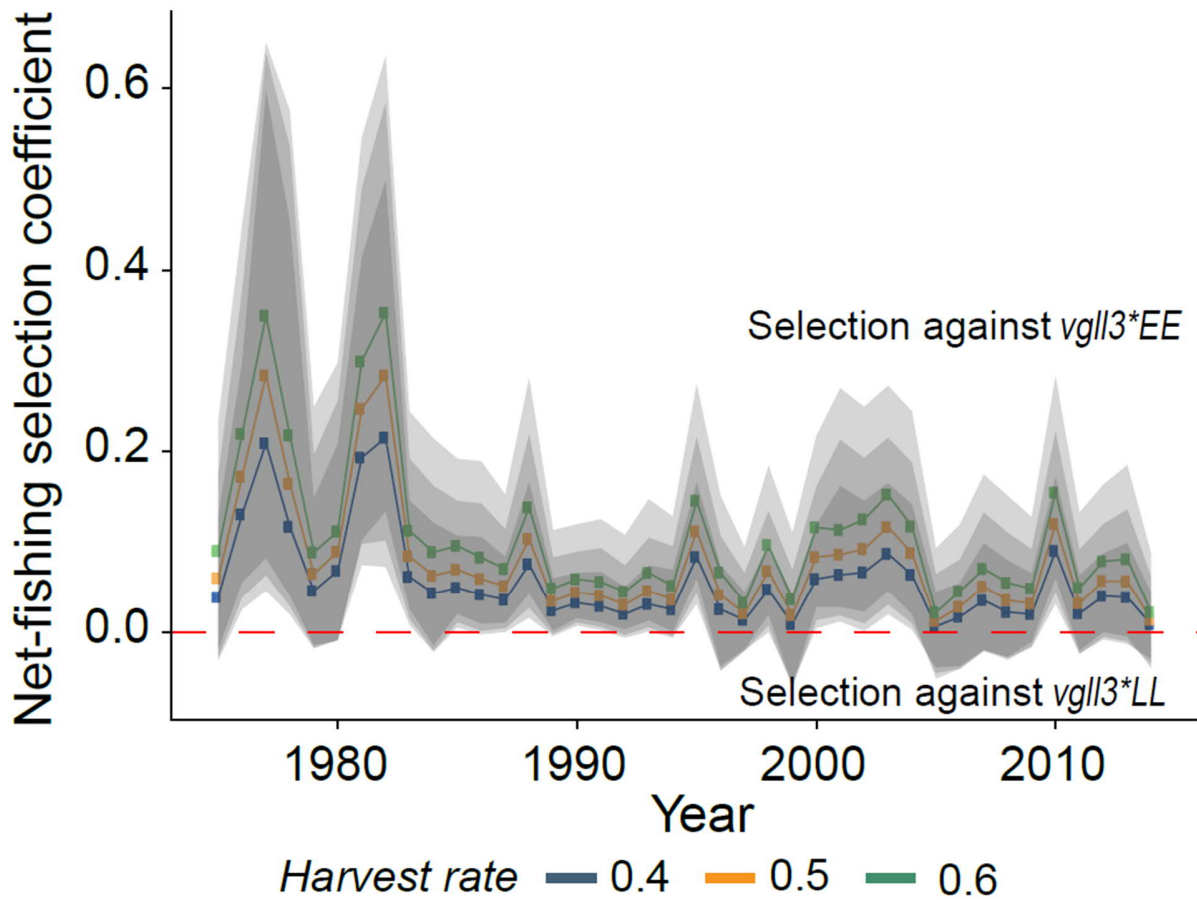
**Fig. 2. Temporal changes in *vgll3*\**L* (later maturation) allele frequency.** The black dotted line represents the observed data, the red line the allele frequency estimated from the final model including the direct and indirect effects of fishing, and the blue line the expected *vgll3*\**L* allele frequency assuming no capelin fishing (annual effect on returning salmon). Black arrows indicate years when there was a moratorium on capelin harvesting (harvest rate < 0.5 percent). As *vgll3* allele frequencies are based on hatch date, capelin fishing closures are expected to impact *vgll3* allele frequencies of salmon hatching a few years earlier than the fishing closures, due to salmon spending 3-5 years in fresh water before migrating to sea. Shaded areas indicate 95% bootstrap intervals based on 3000 replicates (see methods for details).

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5 **Fig. 3. Predicted variation of net-fishing-induced selection over 40 years in Teno salmon as a function of harvest rate.** The selection coefficient corresponds to the difference in relative survival between *vgll3\*EE* and *vgll3\*LL*. Calculations are based on capture probabilities (with harvest rates ranging from 40-60% of returning individuals) as a function of length, using sonar data in 2018 and 2019. It accounts for the sex-specific *vgll3* association with length during the study period, temporal variation in sex-ratio and relative use of the weir, driftnet and gillnet. Shaded area represents 95% confidence intervals based on 6000 iterations.

## Supplementary Materials for

### Rapid evolution in salmon life-history induced by direct and indirect effects of fishing

Y. Czorlich, T. Aykanat, J. Erkinaro, P. Orell, & CR. Primmer\*

Correspondence to: craig.primmer@helsinki.fi

#### This PDF file includes:

Materials and Methods  
Figs. S1 to S8  
Tables S1 to S4

#### Materials and Methods

##### Sampling, genotyping and population assignment

The Teno river (Deatnu in Sámi, Tana in Norwegian), located at the border between Finland and Norway and draining into the Barents Sea (68 - 70°N, 25-28°E), hosts large and diverse Atlantic salmon populations (17, 25). Scales of more than 150,000 salmon caught in different parts of the Teno river system have been collected since 1971, along with individual information including sex, length, weight, sea age at maturity, fishing gear (driftnet, weir, gillnet or rod) and fishing location. Of these, around 113,000 were collected in the mainstem, the focal region of this study. Teno salmon can remain from 2 to 8 years in fresh water before migrating to the sea. They then stay in the marine environment, where most growth occurs, for mostly 1 to 3 years, occasionally 4 or 5, before maturing and returning to spawn (17). Details about sample collection, DNA extraction, genotyping (at 191 SNPs, including *vgll3*, and a sex marker, *sdY* (26)) and population assignment are described in (9). Briefly, a total of 1319 individuals genetically assigned to the Tenojoki population in the middle reaches of the mainstem of the river system (hereafter Teno) in (9) were used in this study, resulting in an average annual sample size of 33 individuals per year between 1975 and 2014. Selected individuals had been caught by rod (the least size selective harvest method (27)) at the end of the fishing season (from 20 July to 31 August), when most of adult salmon are expected to have reached their home river after their sea migration, independently of their sex and life history (28) and thus provides an unbiased sample of the entire spawning population in terms of sex and sea-age-at maturity proportions. The average difference in sea age at maturity between individuals returning to the Teno river that were homozygous for the late vs early genotypes at the large-effect *vgll3* locus (8) was 1.15 year in males and 0.72 year in females.

### Environmental variables

Evolution of age at maturity can be driven by factors occurring either in the freshwater or marine phases of salmon life history. Changes in pelagic communities of the Barents Sea may affect Atlantic salmon survival and life history traits during the marine feeding phase (e.g. 29, 30). The annual stock biomass of important salmon prey species (capelin, herring and krill) has been monitored for decades in the Barents Sea. Data about krill biomass (1980 – 2013) were taken from (31, 32). Capelin biomass estimated from acoustic survey and the landed capelin catches were derived from (33) for 1973 – 2013. Herring dynamics has been estimated using a virtual population analysis (VPA) over the last decades (34). Because herring migrate out of the Barents Sea once they mature, at the age of 3-5 years (35), only the biomass of 1-2 year old herring were used here (e.g. 14). These herring biomass data were retrieved from (34) for the 1973-1998 period. Herring biomass was calculated from the number of 1-2 year old herring and the mean weight per age as reported in (33) for 1988 – 2013. The Pearson correlation between biomasses from those two datasets of herring was 0.99 for the overlapping period, despite values in (33) being lower by a factor 1.46. The data from (34) were standardized, accordingly, by dividing them by 1.46. Data about several species interacting with salmon prey were also used in the multi-species model (see below). The annual biomass of cod (a predator of forage fish) was derived from VPA analyses ((36), table 3.24). Landed cod biomass was also taken from (36). Further, an index for mesozooplankton (a forage fish food source) corresponding to the sum of *Calanus* biomass indices from different parts of the Barents Sea was used (37). Marine temperature has often been associated with growth, age at maturity, or survival in Atlantic salmon (38, e.g. 39). The annual sea temperature in the Kola section of the Barents Sea measured in the upper 200 meters was therefore included (from [pinro.vniro.ru](http://pinro.vniro.ru), (40)).

Salmon fisheries targeting adult salmon returning from their marine migration occur both in the coastal areas around the outlet of the Teno River in northernmost Norway (i.e. the Finnmark region), and in the river using fishing gears with varying degrees of selectivity on size, and hence, age at maturity (17, 41). The total number of nets used to catch salmon in the Finnmark coastal region was calculated for each year using data from (42) whereas the annual number of net-fishing licenses, corrected for the number of fishing days allowed per week (which changed from four days to three days in 1980) was used as a surrogate for riverine net-fishing effort. The corrected number of net-fishing licenses had an among years Pearson's correlation of 0.78 ( $t_{34} = 7.35$ ,  $P$ -value  $< 0.001$ ) with the actual number of weirs in use in the Teno river, estimated from count data during the 1976-2014 time period and adjusted for the number of fishing days in a week (data from years 1980 to 1982 were missing for the latter). Therefore, as the data for net licenses (irrespective of gear type) didn't have any missing data, and covered all gear types, it was used in analyses.

In 2018 and 2019, a sonar count provided an estimate of the size distribution of ascending salmon across the fishing season, thus enabling an estimation of the size selectivity of different riverine fishing methods via comparison with the size distribution of salmon caught with each fishing gear type during the fishing period in June and July. An ARIS explorer 1200 sonar unit (Sound Metrics Corp., Bellevue, Washington, USA) was placed c. 55 km upstream of the Teno river mouth in 2018 and 2019. Only individuals with a length greater than 43 cm were considered as salmon, because of the occurrence of other fish species which are mostly smaller than salmon. Adult salmon are mostly larger than 43 cm in Teno. In fish above 43 cm, other species than salmon occur

to some extent, but their contribution is small. The number of upstream migrating salmon was calculated as the difference between the number of ascending and descending individuals. For the 2019 year class, the total number of salmon in the 136 cm size group was adjusted from minus one (meaning overall, one more fish in the size group descended than ascended in the sonar reading), to zero. The length of salmon caught in 2018-2019 with driftnet, weir, gillnet and rod was recorded by fishers (N = 17, 745, 95 and 219 in 2018 and N = 45, 717, 71 and 334 in 2019; respectively). Salmon lengths from two years of sonar data and catches in these years were grouped in 2 cm bins from 44 cm to 151 cm and used for estimating selectivity of different fishing methods (see below). A small number of individuals that were erroneously estimated to be larger than 150 cm in the 2018 sonar count (N = 17 out of 13,124) were grouped with the last size class bin (no salmon was >150 cm in 40 years of catch data). One 136cm rod-caught individual was moved to the 134-135cm bin in 2019 as no individual of that size class was observed by sonar in that year.

### Statistical analyses

#### *Driver of *vgll3* evolution*

To identify the environmental drivers of *vgll3* evolution, the proportion of *vgll3*\*L alleles (0, 0.5 or 1) in an individual was regressed using a Generalized Linear Model (GLM) with the quasi-binomial family (e.g. 10). Potential departure from Hardy-Weinberg equilibrium, influencing the within-subject covariance of the two alleles, is captured by the overdispersion parameter of the quasi-binomial model (e.g. 14). The sea environment experienced by each individual differs according to their life history strategy (i.e. the specific years an individual spends in the fresh water and marine environments). The prey biomass (krill, capelin and herring) and sea temperature were thus averaged over the year(s) each individual spent in the marine environment (i.e. from the first year to the last full year spent at sea), which was inferred from scale growth ring information. The logarithm of each prey's biomass was included as an independent variable to allow non-linear associations with the *vgll3* proportions and a better correspondence with the multispecies model described below. Annual estimates of the mean sea temperature, the number of coastal fishing nets, the number of tourist rod-fishing licenses (days<sup>-1</sup>) and net-fishing licenses in the Teno river, corrected for the number of permitted weekly fishing days, were also included as predictors. Model selection was performed with a hypothesis testing approach using backward selection with F tests. Statistical tests throughout the study were two-tailed, using an alpha value 0.05 and were performed using R (43). The AICc of all possible models were also calculated along with the relative importance of the different variables, using the MuMIn package (44). The top ranked model based on the AICc had an Akaike weight of 0.22, indicating model uncertainty. It included the number of riverine net and rod licenses, capelin, krill, herring (log) biomasses and temperature covariates. The number of riverine net licenses, capelin, krill and herring were all included in the five other models within a  $\Delta$ AICc less to two to the top ranked model. Model parameters were averaged with the conditional method over 16 models having a summed weight of 0.95 (Table S1). The dispersion parameter was 0.89 in the full model. The maximum variance inflation factor of model parameters was 3.79 (for the number of nets at sea), which is below the frequently recommended thresholds. For graphical representations, fitted allele frequencies were averaged per hatching year and bias-corrected and accelerated bootstrap intervals (BCa) were calculated with the BOOT package (45).

Co-occurrence of temporal trends in both the dependent and independent variables may lead to spurious detection of environmental effects. To account for this, de-trending of the data was

5 achieved as advised in (46) by conducting residual regression on the original data (11). To do this, the independent variables included in the GLM were regressed in a linear model against years and squared years to estimate linear and quadratic trends, respectively. The squared year term was then removed from the model if not significant (assessed by F tests). Residuals of these models then replaced the original independent variables. The GLM described above was re-run by including an additional spawning year effect to remove temporal trends in *vgll3* allele frequency. The spawning year was kept as a covariate during the model selection process even if it was not significant.

#### 10 *Drivers of sex-ratio changes*

To identify variables modifying the sex-ratio of returning adults, a binomial GLM was performed by coding the sex of individuals as 0 (male) or 1 (female). The log biomass of prey species, sea temperature, number of coastal fishing nets and number of riverine net and rod (days<sup>-1</sup>) fishing licenses were included as independent variables as previously. Model selection was performed using the Likelihood ratio test (backward variable selection) and the AICc criterion. We found that variables positively associated with the *vgll3*\*L allele frequency were also positively associated with the probability to sample a female (Table S3, Fig. S2). The number of nets at sea was also positively correlated with female proportion ( $\hat{\beta}^* = 0.50$ ,  $\chi^2_{(1)} = 25.20$ , P-value < 0.001, Table S3). Temporal variation in number of nets at sea is particularly influenced by the cessation of marine driftnet-fishing in 1989, the fishing method the most used in the previous period and selecting preferentially 1 sea-winter and small 2 sea-winter (41), corresponding mainly to males in this system. This analysis was repeated by using the residual regression method to account for potential co-occurrences of temporal trends in the dependent and independent variables, as described above. In the de-trended model, the number of riverine net licenses was not significantly associated with female proportion (Table S3), however the number of rod fishing licenses became marginally positively associated with the probability to sample a female (Table S3). Four models accounting for greater than 0.95 AICc weight were used in the model averaging.

#### 30 *Drivers of changes in age at maturity*

Age at maturity of individual salmon was regressed in a multinomial model using all the independent variables described above (R package nnet (47)). Additionally, *vgll3* genotype and sex were included in the model in a two-way interaction, due to known *vgll3* sex-specific effects (8). Two individuals that matured after five years at sea were pooled with the group having matured after four years at sea. Variable selection with F tests and AICc model averaging over seven models (Table S2) was also performed. This analysis was repeated using the residual regression method. After controlling for sex-specific genetic effects, we found that the same variables positively associated with *vgll3*\*L were also positively associated with the probability to observe older, later maturing Atlantic salmon (Table S2). The total number of nets at sea was also positively associated with later maturation probabilities ( $\chi^2_{(3)} = 11.96$ , P-value = 0.008, Table S3). However, the number of nets at sea and the number of riverine net-fishing licenses were no longer significant in the de-trended regression ( $\chi^2_{(3)} = 3.07$ , P-value = 0.381,  $\chi^2_{(1)} = 4.56$ , P-value = 0.207, respectively; Table S2). The model obtained with backward variable selection also obtained the highest AICc, with a  $\Delta$ AICc superior to 3, indicating strong support.



*Indirect evolutionary effects*

The indirect effect of capelin harvesting on *vgll3* evolution was estimated using the Monte Carlo Method for Assessing Mediation (MCMAM) (48) with capelin (log) biomass as the mediator. The effect of (log) capelin biomass on *vgll3*\**L* odd-ratio was obtained with the quasi-binomial GLM model described above (after backward selection, including the capelin, herring, krill and riverine net-fishing licenses variables). The estimated parameter and standard error were used to generate 3000 samples drawn from a normal distribution. The posterior distribution of the direct effect of harvest rate on the (log) capelin biomass was obtained with the multispecies Gompertz model described below (3 000 MCMC samples, Fig. S4, equation 1), which accounts for effects of, for example, predators, competitors and abiotic factors. The indirect effect of capelin harvest on *vgll3*\**L* odd-ratio corresponds to the product of the two sets of samples (i.e. effect of capelin harvest on (log) capelin x effect of (log) capelin on *vgll3* odds) and thus accounts for uncertainty in both estimates. The indirect effect was also evaluated graphically to account for more than one interaction, by:

- 1) Using the multispecies Gompertz model to predict the biomass dynamics of capelin, herring and krill when capelin harvesting is set to zero from the first year of the time series;
- 2) Using the newly generated data (posterior median) to predict the *vgll3* allele frequency variation using the quasi-binomial GLM obtained with backward selection
- 3) Plotting the temporal allele frequency variation with Bca confidence intervals

This analysis accounted for the effect of capelin harvesting on the biomass of all the Gompertz model species but did not account for *vgll3* evolutionary dynamics (i.e. the propagation of the indirect negative effect from one generation to the next).

*Multispecies Gompertz model*

Fish populations in the Barents Sea have experienced large variation in their abundance over the last 40 years due to fishing and predation (e.g. 13). Consequently, important indirect effects on Atlantic salmon age at maturity variation/evolution may be expected. In order to estimate potential indirect effects, the Barents Sea species interactions, the effect of temperature, density dependence and of cod and capelin fishery were estimated using the multispecies Bayesian Gompertz model developed in (14). To summarize, on the log scale, the process equations were:

$$Cap_{t+1} = a_{cap} + b_{cap}Cap_t + c_{cap,Krill}Krill_t + c_{cap,Cod}Cod_t + c_{cap,Cal}Cal_t + d_{cap}Her_t + e_{cap}T_t + f_{cap}C_{cap,t} + PE_{cap,t} \quad (1)$$

$$Krill_{t+1} = a_{krill} + b_{krill}Krill_t + c_{krill,Cap}Cap_t + d_{krill}Her_t + e_{krill}T_t + PE_{krill,t} \quad (2)$$

$$Cod_{t+1} = a_{cod} + b_{cod}Cod_t + c_{cod,Cap}Cap_t + d_{cod}Her_t + e_{cod}T_t + f_{cod}C_{cod,t} + PE_{cod,t} \quad (3)$$

$$Cal_{t+1} = a_{cal} + b_{cal}Cal_t + c_{cal,Cap}Cap_t + d_{cal}Her_t + e_{cal}T_t + PE_{cal,t} \quad (4)$$

With  $Cap_t$ ,  $Krill_t$ ,  $Cod_t$ ,  $Cal_t$  and  $Her_t$  being the log biomass of capelin, krill, cod, *Calanus* and herring, respectively, in year  $t$ ,  $T_t$  the annual sea temperature in the Kola section of the Barents Sea

at 0-200 m depth (along the 33°30'E meridian from 70°30' to 72°30'N) in year  $t$  and  $C_{Cap,t}$  and  $C_{Cod,t}$  the capelin and cod harvest rates, respectively, in year  $t$  (catch/annual biomass). The coefficients  $a$ ,  $b$  and  $c$  represent the productivity, density dependence and interactions among modelled species, respectively. The coefficient  $d$  represents the interactions with herring,  $e$  the temperature effects,  $PEs$  the multivariate-normal-distributed process errors and  $f$  the fishing effects. A total of 24 process parameters were estimated (Fig. S4). Capelin harvested from the Barents Sea have been used for fish meal and oil from 1914 (49). Capelin use has switched toward human consumption in recent years, notably because of the low total allowable catches (50). The prior distributions in the model were identical to (14) (e.g. uniform prior distributions from -10 to 10 for all process parameters  $a$ ,  $b$ ,  $c$ ,  $d$ ,  $e$  and  $f$ ).

Posterior distributions were approximated using MCMC methods with the Just Another Gibbs Sampler software JAGS (51). The model was run for 1 410 000 iterations including a burn-in length of 710 000. One iteration out of 1000 was kept and 3 chains were run. Convergence was assessed using the Gelman and Rubin's convergence diagnostic and a Potential Scale Reduction Factor (PSRF) threshold of 1.15 (52). The model posterior medians were substituted to the original data for other analyses, in order to replace missing values in krill from 1973 to 1979 and employ common data between the different models used for indirect effect evaluations. Indeed, the multispecies Gompertz model reproduces the observed variation in biomass indices well (Fig. S3). The correlation coefficients between the observed and modelled biomass indices were greater than 0.91. The negative effect of fishing on capelin (log) biomass (standardized  $f_{cap} = -0.39$ ; CI95% = [-0.610, -0.168], Fig. S4) was used to quantify the indirect effect on *vgll3* allele frequency. Capelin dynamics was also influenced by, for instance, krill ( $c_{Cap,Krill} = 0.382$ , CI95% = [-0.030, 0.882]), herring ( $d_{cap} = -0.297$ , CI95% = [-0.549, -0.024]) and cod biomass ( $c_{Cap,Cod} = -0.193$ , CI95% = [-0.496, 0.070]; Eq. 1).

### Net-fishing size selectivity

Teno river local net-fishing encompasses three fishing methods with varying size selectivities (17), due to differences in fishing periods and mesh sizes. Based on traditional knowledge, weirs are typically used in shallower waters than gillnet and driftnet, and have generally smaller mesh sizes. The proportion of salmon maturing after one year at sea was the highest in weir catches in the Teno system, after controlling for the effects of sex, location, year and month of fishing (17). Driftnet fishing is only permitted early in the season (17). The materials used for traditional net-fishing in Teno have not changed greatly over the last decades (17) beside the ban of the small 40-45 mm mesh size (knot to knot) nets from 1989 onwards, which likely targeted early maturing salmon during the first c. 15 years of our time series. To better understand the size selectivity of different fishing gear types and their potential effect on *vgll3* allele frequency changes, we compared the size distribution of salmon caught with each fishing gear type (including driftnet, weir, gillnet and rod) during the fishing period in June and July in 2018 and 2019 to the size distribution of ascending salmon obtained from a sonar count in the river during the same period and years. The number of salmon caught per 2 cm. length class ( $l$ , from 44 to 151 cm) was analyzed for each gear ( $g$ ) with a Generalized Additive Model (GAM) using the beta-binomial family to account for overdispersion. Length of each salmon ( $L$ ) was included as a predictor, in a regression spline ( $s_g$ ):

$$C_{l,g,y} = \alpha_y + s_g(L) \quad (5)$$

With  $C_{l,g,y}$  the mean proportion of salmon caught per 2 cm. length class ( $l$ ) in year ( $y$ ) with the fishing gear ( $g$ ) and,  $\alpha_y$  the annual intercepts with priors following a normal distribution (mean = 0, sd = 10). The dispersion parameters of the beta distribution (i.e. addition of both shape parameters) followed a prior uniform distribution between 2.5 and 5000 for each gear. The priors, code and associated data for the smooth part of the model were generated with the R package *mgcv* (see (53) for more information). The model was run in JAGS (51) (R package *runjags* (54)) for 7 600 000 iterations including a burn-in period of 4 000 000. Two chains were run and one iteration out of 1200 was kept. Convergence was checked using the Gelman and Rubin's convergence diagnostic (52) and inspection of trace plots.  $C2_{i,l,g}$ , used below, corresponds to the mean capture probability of the gear ( $g$ ) per 2 cm. length class ( $l$ ) calculated at each iteration ( $i$ ) from the model estimates, and divided by  $\sum_{l=1}^{54} C2_{i,l,g}$  so that it sums to one over the different length groups.

### *Temporal variation in riverine net-fishing selection on *vgll3**

The effect of riverine net-fishing on *vgll3* allele frequency depends on the size selectivity of the fishing gears, calculated above (Fig. S6), the harvest rate per fishing gear, and distribution of *vgll3* genotypes according to salmon size. The number of salmon genetically assigned to the Teno mainstem population was modelled with a GAM using the negative binomial family, to allow for over-dispersion. Length was included as an independent variable inside annual random smooths, to account for changes in age at maturity over time. All GAM models in the following part of the method were run using the *mgcv* package (55). To account for uncertainty, simulations from the posterior distribution of the fitted model were performed by using a Metropolis Hastings sampler (56) (8 chains, 300 000 iterations per chain, thinning of 400, burn-in of 1000). For each iteration ( $i$ ), the proportion of salmon in the different 2 cm length classes ( $Pl_{i,l,y}$ ) was calculated for each year ( $y$ ) from the model predicted values. Those proportions were later used to estimate the gear-specific fishing mortality to match the expected gear-specific annual harvest rates (see below).

A model including annual random smooths per sex was also used to estimate  $Pl2_{i,l,s,y}$ , the proportion of salmon in the different 2cm length class per sex and year at each iteration ( $i$ ) (Metropolis Hastings sampling with 8 chains, 300,000 iterations per chain, thinning of 400, burn-in of 1000). The median length-frequency distributions of harvested salmon calculated from negative binomial GAM fitted values differed between sexes (Fig. S8a). Females measuring around 97 cm were the most frequent whereas most frequent males measured around 60 cm. There was among-year variation in the length-frequency distribution, particularly in males, where large individuals were more frequent in the early years of the time series. The negative binomial parameter controlling the over-dispersion was 7.31.

The proportion of salmon caught by each fishing gear over the 40-year period ( $Pr_{y,g}$ ) was estimated from the annual catch weight and converted to an estimate of the individual number using the annual average weights of salmon caught in the mainstem with the different gears (N = 84 452). There was no clear trend in the proportion of salmon caught with the different fishing gears in Teno across the time series (57). The total harvest rate ( $HR_{tot}$ ) was fixed at either 40%, 50% or 60% (as riverine fishing mortality of up to 69% on tagged salmon has been reported (58)), only the gear specific harvest rate ( $HR_{exp,y,g}$ ) being allowed to vary over time according to the previously calculated proportions ( $Pr_{y,g}$ ):



$$HR_{exp_{y,g}} = Pr_{y,g} HR_{tot} \quad (6)$$

Given that fishing with the different gears occurs simultaneously, the instantaneous fishing mortality needed to be estimated according to the expected harvest rate ( $HR_{exp_{y,g}}$ ) and gear size selectivity ( $C2_{i,l,g}$ ). A modified version of the Baranov's catch equation was used to calculate the harvest rates ( $HR_{i,y,g}$ ) of the gear ( $g$ ) in year ( $y$ ) at each iteration ( $i$ ):

$$HR_{i,y,g} = \sum_{l=1}^{54} \left( 1 - e^{-(\sum_{g=1}^4 F_{i,l,y,g})} \right) \frac{F_{i,l,y,g}}{\sum_{g=1}^4 F_{i,l,y,g}} Plcorr_{i,l,y} \quad (7)$$

With  $Plcorr_{i,l,y}$  the proportion of salmon in the 2 cm. length class ( $l$ ) in year ( $y$ ) at iteration ( $i$ ) before fishing ( $Plcorr_{i,l,y} = \frac{Pl_{i,l,y}}{e^{-(\sum_{g=1}^4 F_{i,l,y,g})}}$ , modified to sum to one over the length classes).  $F_{i,l,y,g}$  is the instantaneous fishing mortality for the length class ( $l$ ), gear ( $g$ ) and year ( $y$ ) calculated at each iteration from the mean capture probabilities  $C2_{i,l,g}$ :

$$F_{i,l,y,g} = -\log(1 - C2_{i,l,g} \beta_{i,y,g}) \quad (8)$$

$\beta_{i,y,g}$  was determined by minimizing  $D = \sum_i^4 (HR_{i,y,g} - HR_{exp_{y,g}})^2$  using the R `optim` function from the `stats` package with the "L-BFGS-B" method (59) and a lower bound of 0.01. The Nelder-Mead method was used if convergence was not achieved with the "L-BFGS-B" method (12 iterations), while ensuring that  $\beta_{i,y,g}$  was positive (e.g. by squaring it). The maximum instantaneous fishing mortality was capped at 2.30, allowing a maximum harvest rate per fishing gear equal to 0.95. This was used to avoid unrealistic correction, at some iterations, of the length-frequency distribution when calculating  $Plcorr_{i,l,y}$ .

The exploitation rates per year ( $y$ ), *vgll3* genotype ( $v$ ) and net-fishing gear ( $g$ ) were then calculated at each iteration ( $i$ ) as follows:

$$ER_{i,y,v,g,s} = \sum_{l=1}^{54} \left( 1 - e^{-(\sum_{g=1}^4 F_{i,l,y,g})} \right) \frac{F_{i,l,y,g}}{\sum_{g=1}^4 F_{i,l,y,g}} Plg_{i,l,y,s,v} \quad (9)$$

With  $Plg_{i,l,y,s,v}$  the proportion of individuals of sex ( $s$ ) in the 2 cm. length class ( $l$ ) in year ( $y$ ) and with the *vgll3* genotype ( $v$ ), calculated at each iteration ( $i$ ) as follow:

$$Plg_{i,l,y,s,v} = \frac{Pl2corr_{i,l,y,s}}{\sum_{l=1}^{54} Pl2corr_{i,l,y,s}} Pvgl3_{i,l,s} \quad (10)$$

And modified to sum to one over the length class.  $Pl2corr_{i,l,y,s}$  is the proportion of individuals of sex ( $s$ ) in the length class ( $l$ ) in year ( $y$ ) before fishing, calculated at each iteration ( $i$ ) from the length distribution previously estimated with the GAM:

$$Pl2corr_{i,l,y,s} = \frac{Pl2_{i,l,y,s}}{e^{-(\sum_{g=1}^4 F_{i,l,y,g})}} \quad (11)$$

$Pvgl3_{i,l,s}$  corresponds to the probability of the different *vgll3* genotypes for a salmon in the 2 cm length class ( $l$ ) and sex ( $s$ ; Fig. S8b). This probability was estimated with a multinomial GAM including the 2 cm length classes in a regression spline for each sex and genotype. Posterior simulations (1 chain, 6 000 000 iterations, thinning of 1000, burn-in of 1000) were performed using the Metropolis Hastings sampler. Alternative models allowing the smooth parameter to change per sex and decades in one or both of the modelled genotypes were also run. There was no evidence for changes in the length-specific probability of the different *vgll3* genotypes over time

(model fitted with maximum likelihood,  $\Delta AIC > 8$  and LRT test P-value = 0.096 with the best competing model).

Finally, the mortality per genotype ( $v$ ) and year ( $y$ ) for the 3 net-fishing methods in the population corresponded to:

$$M_{i,y,v} = \sum_{g=1}^3 ER_{i,y,v,g,s=female} SR_{corr_{i,y,v}} + \sum_{g=1}^3 ER_{i,y,v,g,s=male} (1 - SR_{corr_{i,y,v}}) \quad (12)$$

The mortality per genotype accounts for temporal variation in the proportion of females per genotype before fishing ( $SR_{corr_{i,y,v}}$ ). Temporal variation in the female salmon proportion was analysed with a quasi-binomial GAM, including year as an independent variable inside a cubic regression spline for each genotype and adding an extra penalty to each term. To account for uncertainty, simulations from the posterior distribution of the fitted models were performed by randomly drawing 6000 values from a multivariate normal distribution with the mean vector and the covariance matrix equal to the model estimates. The GAM fitted values were calculated at each iteration to obtain  $SR_{i,y,v}$ . The proportion of females before fishing corresponded to:

$$SR_{corr_{i,y,v}} = \frac{(1 - \sum_{g=1}^4 ER_{i,y,v,g,s=male}) SR_{i,y,v}}{1 - \sum_{g=1}^4 ER_{i,y,v,g,s=female} (1 - SR_{i,y,v}) - \sum_{g=1}^4 ER_{i,y,v,g,s=male} SR_{i,y,v}} \quad (13)$$

The decrease in proportion of females with the  $vgll3*EE$  genotype over time was linear (GAM smoothing term was not significant; edf = 0.45, F = 0.05, P-value = 0.171). The decrease in the proportion of females with  $LL$  genotype over time was slightly non-linear (edf = 1.32, F = 0.33, P-value = 0.001) whereas the proportion of  $EL$  females mainly declined during the 1980s and in the last 7 years of the time series (edf = 6.25, F = 2.07, P-value < 0.001). The dispersion parameter of the quasi-binomial GAM was 1.52.

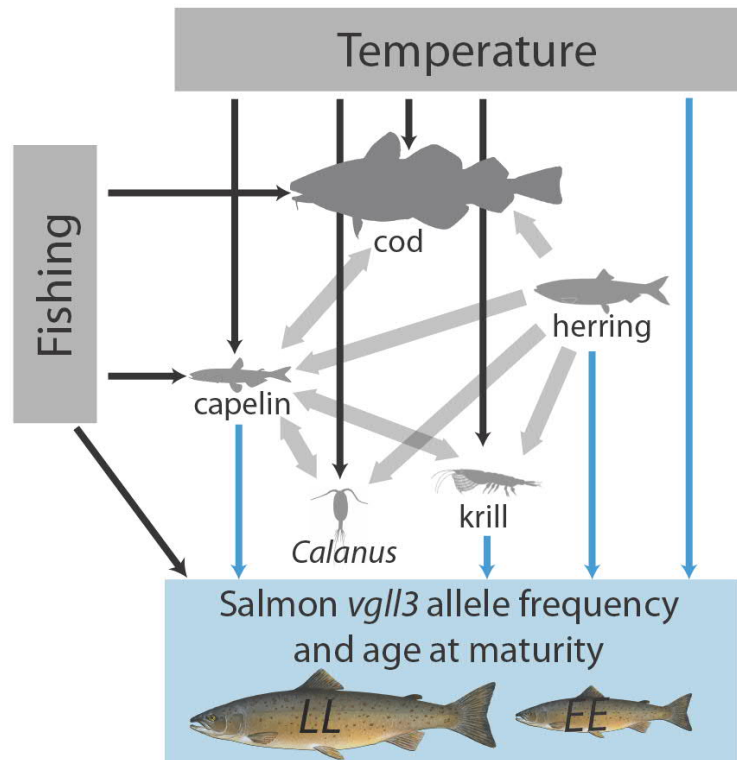
The survival of the different genotypes could then be calculated:  $W_{i,y,v} = 1 - M_{i,y,v}$  (Fig. S7). On average, the annual relative difference in mortality was higher in males than females for fishing gears selecting against  $vgll3*LL$  (i.e. driftnet, gillnet and rod) but lower for weir fishing selecting against  $vgll3*EE$ . Fishing mortality of  $vgll3*LL$  was on average 52% lower than  $vgll3*EE$  when weir was used but 27-29% higher when driftnet, gillnet or rod were used.

The annual fishing selection against the less fitted homozygote ( $S_y$ ) was calculated as follows:

$$S_{i,y} = 1 - \min(W_{i,y,1}, W_{i,y,3}) / \max(W_{i,y,1}, W_{i,y,3}) \quad (14)$$

The sign of  $S_y$  was changed according to  $\max(W_{i,y,1}, W_{i,y,3})$ ;  $S_y$  is positive when  $W_{i,y,1} < W_{i,y,3}$  and negative otherwise. Calculations of variation in selection and relative mortality assume temporally constant gear selectivity. The total harvest rate is also assumed constant over time and was included to assess whether the fishing pressure in the Teno river is strong enough to induce significant selection. Selection against  $vgll3*EE$  before 1989 is potentially underestimated due to the ban of the small 40-45 mm mesh size from 1989 on, which is not accounted for in our model.

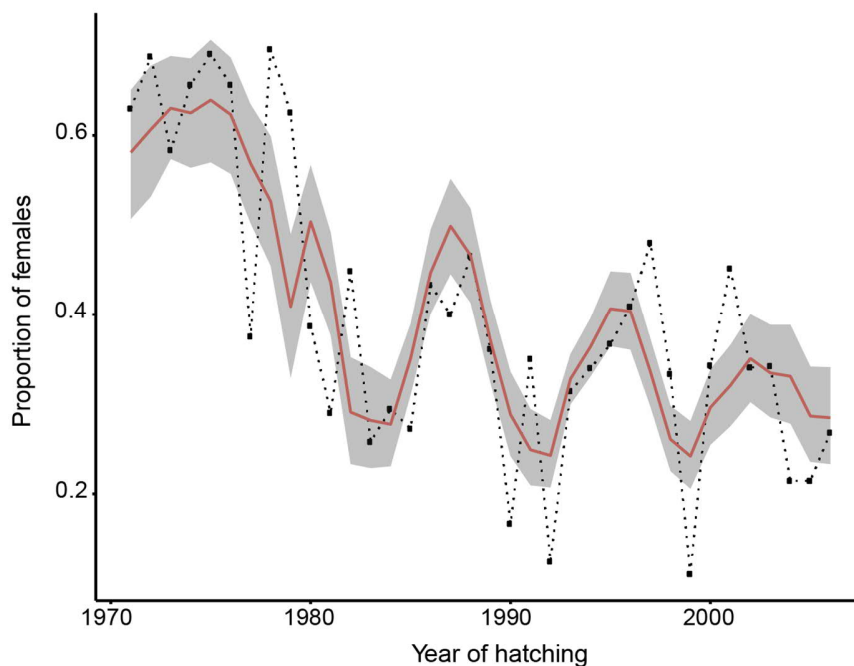
Effect of riverine net-fishing selection on  $vgll3$  (using constant harvest rate equal to 0.5) were then investigated in a post-hoc analysis. The previous  $vgll3$  normal and de-trended quasi-binomial GLMs were re-run by including  $S_{i,y}$  as an independent variable (Table S4).



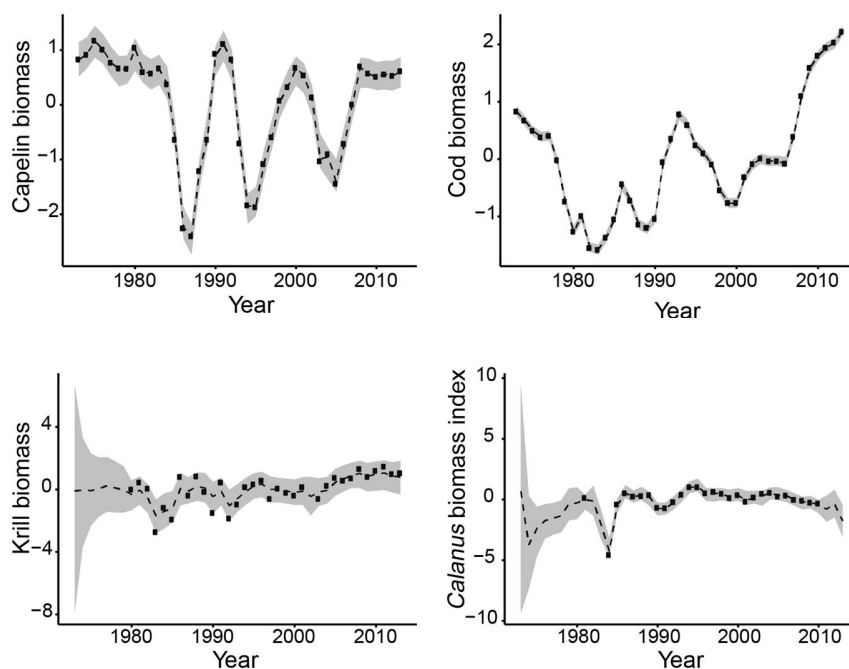
**Fig. S1. Barents Sea ecosystem model applied for detecting indirect evolutionary effects.**

Interactions in the Barents Sea community are as modelled by (14), plus customized links with Atlantic salmon age at maturity and *vgll3* allele frequencies. The grey arrows represent uni- or bi-directional interactions among key species of the Barents Sea, the blue arrows indicate the variables from the multispecies model directly included in the regression of salmon *vgll3* allele frequencies and age at maturity and the black arrows the potential effects of other factors such as fishing.

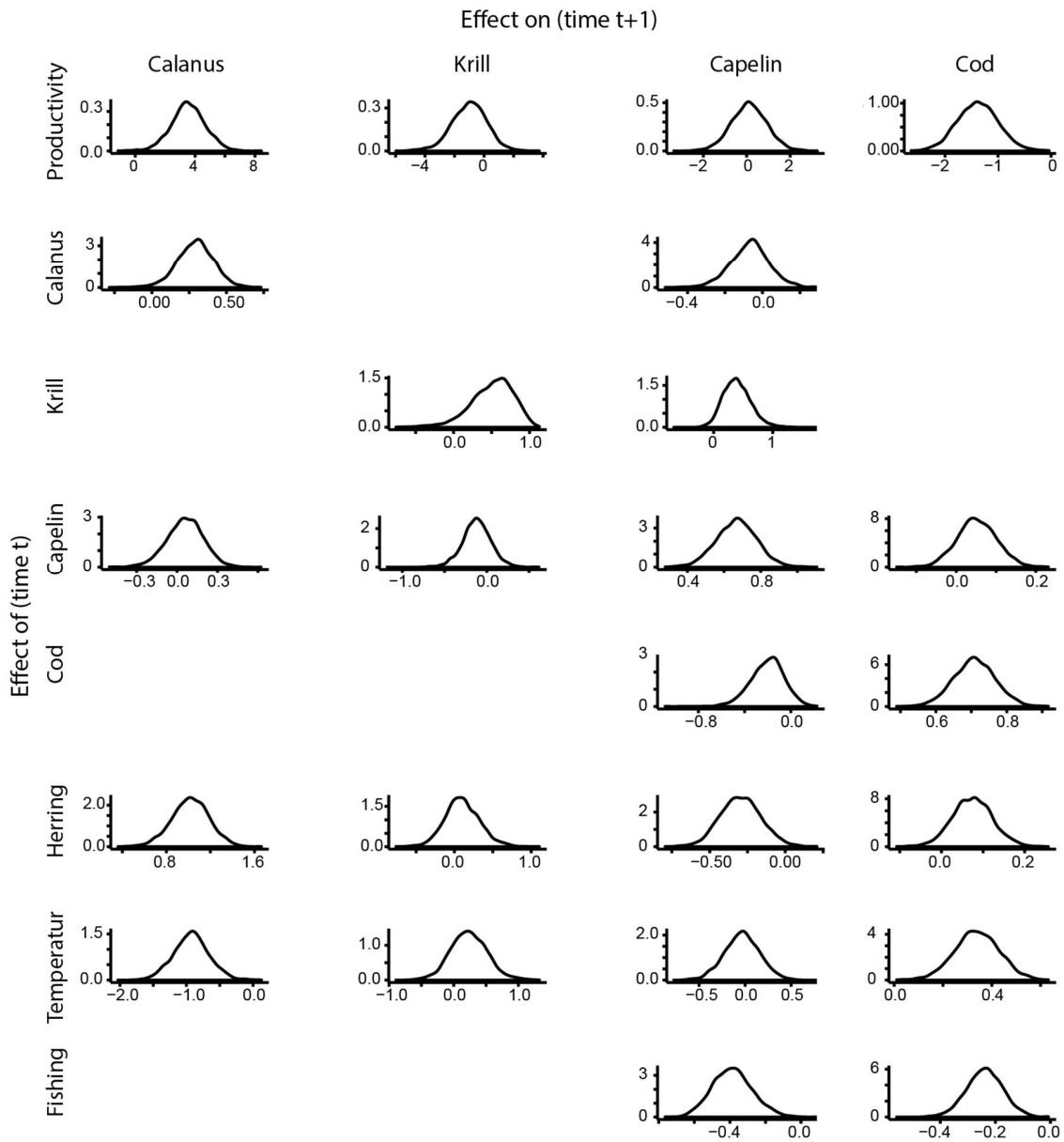
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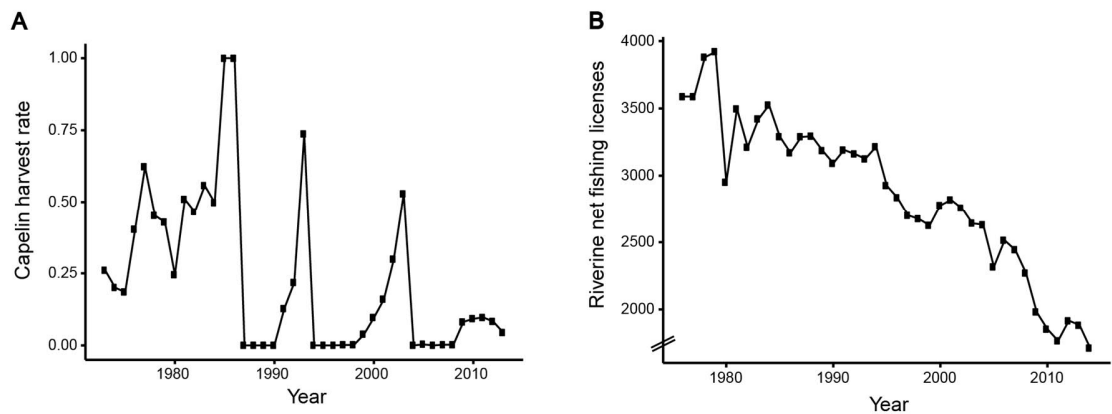
**Fig. S2. Temporal changes in proportion of females over 36 hatching years.** The black dotted line represents the observed data, the red line the female proportion averaged from individual fitted values. Confidence intervals are bias-corrected and accelerated (BCa) 95% bootstrap interval based on 3000 replicates.



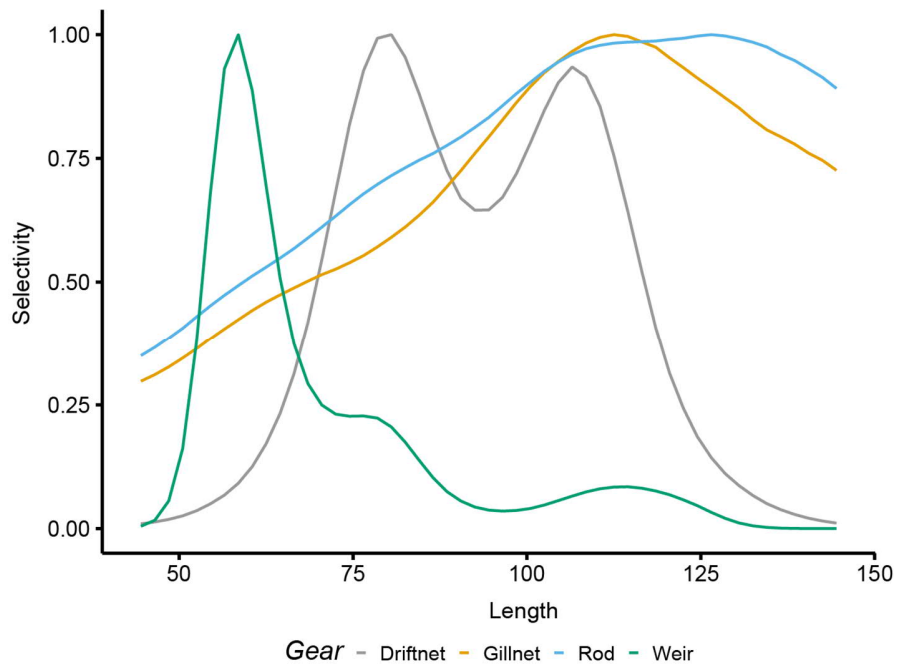
**Fig. S3. Annual variation in log transformed and normalized biomass of capelin, cod, krill and, *Calanus* in the Barents Sea.** The dots represent the observed data, the dashed lines the model posterior medians and the shaded areas the 95% credible intervals.



**Fig. S4. Posterior probability distribution of process parameters included in the multispecies Gompertz model.**

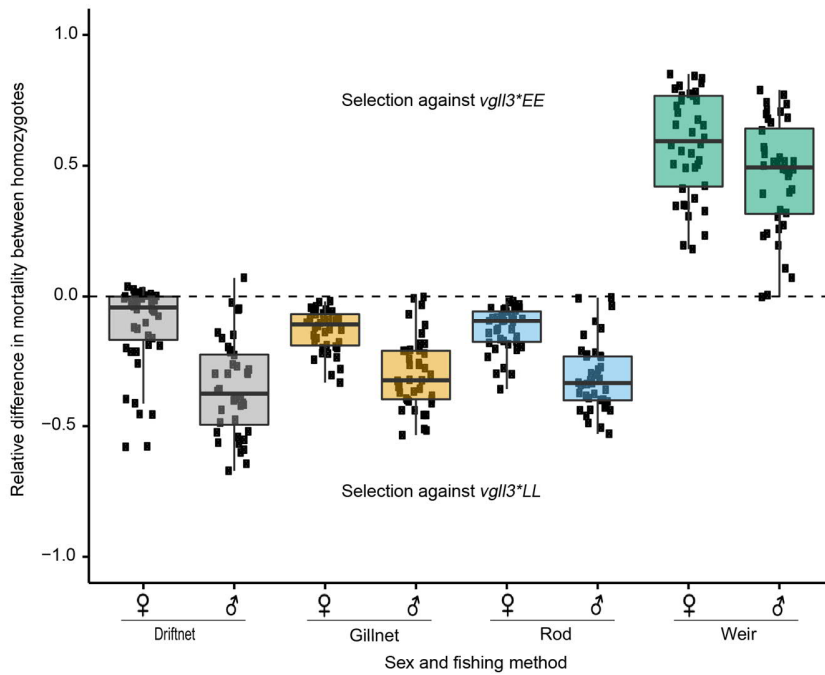


**Fig. S5. Temporal variation in fishing related indices.** *A*, capelin harvest rate. *B*, corrected riverine net-fishing licenses (number of licences multiplied by effective number of fishing day per week).



**Fig. S6. Bayesian posterior median selectivity of the different gears as a function of salmon length (in cm).** Median capture probabilities were transformed so that selectivity curves peak at 1. Weir selectivity was bell-shaped with a modal value of 58 cm. Driftnet selectivity was bimodal with modal values of 80 and 107 cm. Gillnet and rod had sigmoid selectivity curves with capture probabilities increasing with salmon length until reaching maxima at 112 and 126 cm, respectively.





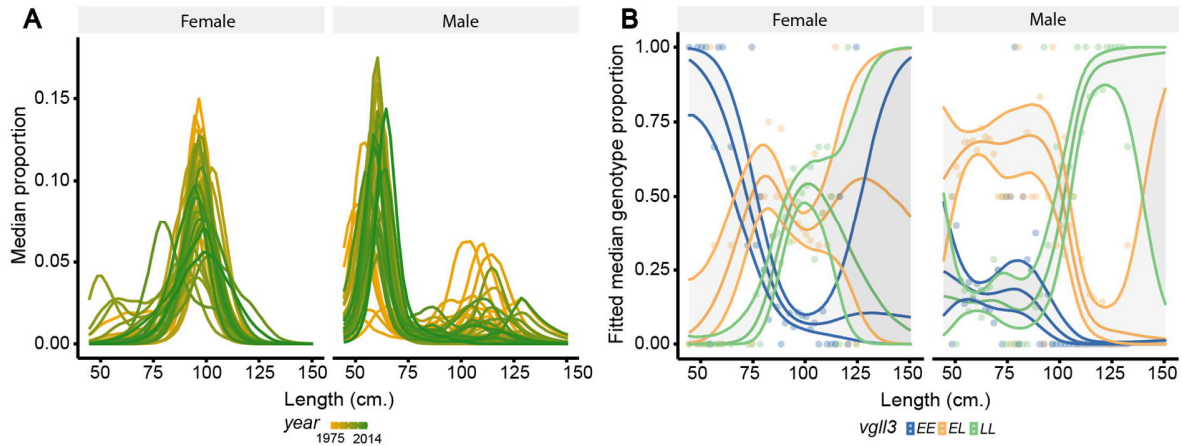
**Fig. S7. Median annual relative difference in mortality between alternative *vgll3* homozygotes (black squares) for different fishing gears in male and female Atlantic salmon.** Positive values indicate higher mortality in the *vgll3\*EE* genotype than in the *vgll3\*LL* genotype, negative values represent higher mortalities in the *vgll3\*LL* genotype. Boxplots display the minimum value (median – 1.5 interquartile range), 25<sup>th</sup> percentile, median, 75<sup>th</sup> percentile and the maximum value (median + 1.5 interquartile range).

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**Fig. S8. Median proportion of A, salmon per length class, sex and year genetically assigned to the Teno population between 1975-2014 and B, *vgll3* genotypes per length class and sex.** Median proportions were calculated using metropolis Hastings sampling from A, a negative binomial GAM and B, a multinomial GAM (6000 iterations kept). Shaded area represents 95% confidence intervals.

**Table S1. AICc relative importance (RI), model averaged standardized estimates, unconditional standard errors (SE), and hypothesis testing F-tests for the 7 predictors included in the *vgll3* allele frequency (quasi)binomial regressions.**

	RI	Estimate (log-odds)	SE	F <sub>(1)</sub>	P-value	Detrended	
						F <sub>(1)</sub>	P-value
River net licenses	1.00	0.40	0.09	27.79	< 0.001	14.15	< 0.001
Capelin log	1.00	0.20	0.06	20.77	< 0.001	10.64	0.001
Krill log	0.91	0.19	0.07	6.42	0.011	2.05	0.153
Herring	0.88	0.19	0.08	9.30	0.002	3.23	0.072
River licenses	rod 0.69	0.15	0.08	1.55	0.213	0.62	0.431
Temperature	0.56	-0.11	0.07	2.88	0.090	2.63	0.105
Nets at sea	0.37	0.08	0.08	0.91	0.341	0.12	0.725
Intercept	-	0.37	0.04	-	-	-	-
Year	-	-	-	-	-	18.98	< 0.001

**Table S2. AICc relative importance (RI), model averaged standardized estimates, unconditional standard errors (SE), and hypothesis testing LRT-tests for the 9 predictors potentially influencing age at maturity probability in salmon individuals in the dataset (multinomial model).**

	RI	2 years vs 1 year		3 years vs 1 year		4 years vs 1 year		LRT	P- value	De-trended model	
		estimate	SE	estimate	SE	estimate	SE			LRT	P- value
River net licences	1.00	-0.14	0.26	0.93	0.22	0.48	0.31	28.9	<0.001	4.56	0.207
Capelin log	1.00	-0.11	0.15	0.51	0.14	0.8	0.24	26.43	<0.001	20.70	<0.001
Krill log	1.00	0.10	0.22	0.99	0.21	0.92	0.32	34.04	<0.001	22.94	<0.001
Herring	0.97	0.17	0.22	0.71	0.24	0.96	0.4	14.56	<0.001	28.71	<0.001
River rod licences	0.81	0.31	0.21	0.31	0.19	-0.47	0.31	9.79	0.020	16.89	<0.001
Temperature	0.22	0.01	0.20	-0.22	0.19	-0.48	0.28	3.33	0.343	10.25	0.027
Nets at sea	0.89	0.38	0.24	0.66	0.21	0.58	0.3	11.96	0.008	3.07	0.381
sex vgll3*EL	1.00	-2.32	0.73	-1.28	1.2	8.25	0.63	23.78	<0.001	24.46	<0.001
sex vgll3*LL	1.00	-1.91	0.98	0.59	1.29	10.8	0.65	23.78	<0.001	24.46	<0.001
sex	1.00	-2.53	0.47	-5.31	1.06	-13.31	0.46	-	-	-	-
vgll3*EL	1.00	1.97	0.63	2.82	0.6	3.61	1.2	-	-	-	-
vgll3*LL	1.00	1.65	0.84	3.63	0.78	4.3	1.3	-	-	-	-
Intercept	-	0.21	0.84	0.78	0.33	-2.89	1.05	-	-	-	-
Year	-	-	-	-	-	-	-	-	-	21.95	<0.001

**Table S3. AICc relative importance (RI), model averaged standardized estimates, unconditional standard errors (SE) and hypothesis testing LRT-tests for the 7 predictors included in the binomial regressions for the probability to sample a female salmon.**

	RI	Estimate (log-odds)	SE	LRT <sub>(1)</sub>	P-value	Detrended	
						LRT <sub>(1)</sub>	P-value
River net licences	1.00	0.52	0.12	22.32	< 0.001	0.35	0.553
Capelin log	1.00	0.40	0.07	34.06	< 0.001	14.28	< 0.001
Krill log	1.00	0.44	0.11	15.94	< 0.001	10.79	0.001
Herring	1.00	0.50	0.11	20.84	< 0.001	24.86	< 0.001
River rod licences	0.30	0.07	0.11	0.55	0.458	4.53	0.033
Temperature	0.32	-0.07	0.10	0.42	0.517	1.70	0.192
Nets at sea	1.00	0.51	0.11	25.20	< 0.001	16.78	< 0.001
Intercept	-	-0.48	0.06	-	-	-	-
Year	-	-	-	-	-	37.27	< 0.001

**Table S4. Parameter estimates, standard errors (SE), and hypothesis testing F-tests for the 8 predictors in the (quasi)binomial regression testing the association between the estimated riverine net-fishing selection (harvest rate = 0.5) and *vgll3* allele frequency.**

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	Estimate (log-odds)	SE	F <sub>(1)</sub>	P-value	Detrended	
					F <sub>(1)</sub>	P-value
Net-fishing selection	0.13	0.05	4.88	0.027	8.97	< 0.001
River net licenses	0.36	0.07	18.52	< 0.001	15.60	< 0.001
Capelin log	0.20	0.05	14.48	< 0.001	7.47	< 0.01
Krill log	0.15	0.06	4.54	0.033	1.29	0.256
Herring	0.21	0.05	11.50	< 0.001	2.30	0.130
River rod licenses	0.09	0.06	1.46	0.228	0.01	0.926
Temperature	-0.08	0.07	1.14	0.286	0.79	0.374
Nets at sea	0.03	0.08	0.11	0.741	0.00	0.973
Intercept	0.38	0.04	-	-	-	-
Year	-	-	-	-	15.17	< 0.001