Quantifying heritable and plastic components of age at maturation in Atlantic salmon and predicting response to selection by fisheries.

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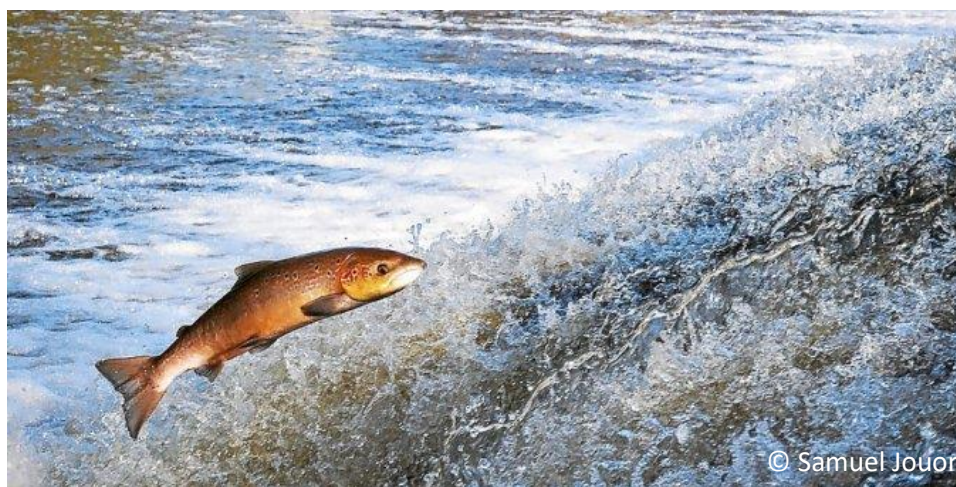
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1SW: One sea-winter: Salmon that have spent one winter at sea before reproduction

2SW: Two sea-winter: Salmon that have spent two winters at sea before reproduction

COLISA: Collection of ichthyological samples coming from long term monitoring and research activities conducted by 3 INRAE units and from a national catch declaration scheme.

DNA: Deoxyribonucleic Acid

H^2: Heritability in the broad sense

h^2: Heritability in the narrow sense

ICES: International Council for the Exploration of the Sea

INRAE: Institut National de la Recherche pour l'Agriculture, l'Alimentation et l'Environnement

IPM: Integral projection model

MCMC: Markov Chain Monte Carlo

PCR: Polymerase chain reaction

WGNAS: Working group on the North Atlantic salmon, ICES

I.   Introduction

Natural populations are subject to multiple anthropogenic and environmental pressures (global change, overexploitation, pollution…) that can impact their demographic structure and their dynamics and that represent a significant threat to global biodiversity over the next century (Butchart *et al.*, 2010 ; Lovejoy and Hannah., 2005 ; Sala *et al.*, 2000 ; Thomas *et al.*, 2004). Migratory species, by travelling large distances and interacting with different habitats are particularly likely to be affected by these pressures at some point in their life cycle (Newson *et al.*, 2009). There is already compelling evidence for impacts on a wide range of birds, marine mammals, fish, insects and other organisms (Robinson *et al.*, 2009). For instance, many avian populations have shifted the timing of their breeding (Nussey *et al.*, 2005) and migration (Pulido *et al.*, 2001) in the last decades in response to environmental changes.

Phenotypic plasticity and micro-evolutionary changes are the two-primary means by which organisms respond to environmental change. Phenotypic plasticity is defined as the ability of an individual's genotype to produce multiple phenotypes in different environments (Pigliucci, 2001, 2005). Phenotypically plastic traits can respond very quickly to altered environmental conditions, especially for seasonal timing of life cycle events (migration, breeding). However, this kind of response could be very costly for the organism (Auld *et al.*, 2010) and are therefore rarely sustainable on a long term. On the other side, evolutionary changes as a response to selection required heritable traits and are generally slower to change phenotypes than plasticity (Hendry et Kinnison, 1999). As an illustrative example, in great tits, the mean egg-laying date has advanced by about 14 days over fifty years, due to phenotypic plasticity (Charmantier et al., 2008). Based on laying date heritability and the selection on this trait, the authors evaluated that the same phenotypic change would have taken two centuries if driven by evolutionary changes only. Because of the costs of phenotypic plasticity, it is thus assumed that microevolutionary change will be necessary to prevent population declines (Lande et Shannon, 1996 ; Phillimore et al., 2010).

Disentangling the actions of evolutionary and plastic changes in response to selection is challenging. Indeed, empirical data needed for disentangling mechanisms are still scarce and consequences at a population level often remain unclear (Charmantier et Gienapp, 2014 ; Knudsen *et al.*, 2011). Numerous papers are reviewing studies trying to understand plastic and evolutionary responses of birds (Knudsen *et al.*, 2011), mammals (Boutin and Lane, 2014) and fish (Crozier and Hutchings, 2014) populations in response to climate change. For instance, Møller (2001) showed that the migration arrival date of the barn swallow (*Hirundo rustica*) was

correlated with the tail length, a heritable trait that should allow a quick response to selection in situations of environmental changes. Réale *et al.* (2003), has shown that the timing of breeding of red squirrel (*Tamiasciurus hudsonicus*) has advanced by 18 days in 10 years. This change in parturition date was explained by a plastic response to increased food abundance although an evolutionary response to selection favoring earlier breeders also contributed to the observed change toward early breeding. Crozier *et al.*, (2008, 2011) studied Chinook (*Oncorhynchus tshawytscha*) and sockeye (*Oncorhynchus nerka*) salmon's migration and spawning date in response to environmental conditions but fail in identifying the relative role of phenotypic plasticity versus heritability due to the lack of data on heritability and selection strength concerning these traits.

Here, we focus on Atlantic salmon (*Salmo salar*, Linnaeus, 1758), an anadromous species of high cultural and scientific importance, reproducing in more than 2000 rivers distributed in Europe and North America. It is an important model in evolutionary and conservation biology providing valuable information on the adaptive response of populations and the effect of anthropogenic changes (Garcia de Leaniz *et al.*, 2007; Aas et al., 2011). In general, salmon spend between one and six years in the river as juveniles before migrating to the sea as smolts. The marine phase generally lasts between one and four years before sexual maturation which triggers the decision to return to its natal river. However, the duration of the river and marine phases varies greatly according to the geographical location of the populations. In the populations of Southern Europe, and particularly in France, juveniles remain between one and two years in river before migrating at sea where they spend between one and two years before maturing and returning to the river (Aas et al., 2011).

Age at maturation is here a key life-history trait with a trade-off between the decision to mature quickly to maximize survival or to delay maturation to maximize fecundity (Mobley *et al.*, 2020 ; Stearns, 1992). Individuals returning after two years at sea will be larger and have a better reproductive potential than individuals maturing in the first year. However, they will also have a higher mortality rate due to the additional year spent at sea. Additionally, this trade-off is likely sex-specific, with females having higher fecundity benefits than male for delaying maturation (Fleming, 1998). This difference between sexes translate into very contrasted sex-ratio among returning salmon with different sea-age: older salmon are predominantly females (ICES, 2021) as in many other salmonids (Holtby et Healey, 1990). Differences in the timing of maturation between males and females have been recently modelled by a sex-specific maturation norm (Tréhin *et al.*, 2021), where the maturation decision is triggered by reaching a

body length threshold at the end of the first summer at sea, with a higher threshold for females than males.

The solution to this sex-specific trade-off between survival and fecundity is variable through space and time and depending on growth conditions in river and in feeding grounds at sea. In general, salmon from northern population (Labrador, Finland, Norway) mature older than salmon from southern populations (France, UK, Ireland, Newfoundland; WGNAS 2021). Additionally, age-at-maturation has varied through time, showing a weak synchrony across populations in the North American and Southern European: it generally decreased from 1970, before reaching a plateau in 1990 and increasing in recent years (ICES, 2021 ; Olmos *et al.*, 2019). In addition to this global pattern, most populations also have specific trends in age-at-maturation (ICES, 2021 ; Olmos *et al.*, 2019).

Investigating the drivers behind those changes is paramount in a context where salmon populations have experienced a sharp decline over the last decades (Limburg et Waldman, 2009 ; Olmos *et al.*, 2019). This decline is generally attributed to a decrease in marine survival (Chaput, 2012 ; ICES, 2021), that have been linked to changes in ocean conditions (Mills *et al.*, 2013 ; Renkawitz *et al.*, 2015). Given that salmon with different age-at-maturation have different migration route and feeding grounds at sea (Dadswell *et al.*, 2010), this life-history trait is key to the survival dynamics. Thus, separating the plastic and genetic component behind variation in age-at-maturation would be invaluable towards understanding past and predicting future dynamics in a context of rapid environmental changes.

Both the plastic (Tréhin *et al.*, 2021 ; Vollset *et al.*, 2022) and the heritable response (Barson *et al.*, 2015 ; Czorlich *et al.*, 2018) of salmon maturation rate have already been heavily studied, although generally separately. Tréhin *et al*. (2021) have shown that the probability to return in freshwater after one year at sea increases as salmon growth increases, highlighting the importance of marine growth during the first summer at sea on the maturation rate. In parallel, by investigating marine growth anomalies in Norwegian populations which are supposed to translate large scale changes in marine growth conditions, Vollset *et al.*, (2022) highlighted a decrease of A. salmon growth along with a decrease of the proportion of early maturing individuals. These changes occurred during a decrease in the extent of Arctic water in the Norwegian Sea leading to a 50% reduction of zooplankton. Similar patterns have also been observed by Tréhin (2022) on southern European populations. These studies suggest a plastic response of this trait to environmental changes. In addition, evolutionary changes could also explain part of the observed change of maturation age in salmon populations. Heritability of

age at maturation has been studied for several decades. Approaches were first made at the individual scale through laboratory experiments (Gjerde, 1984). These crossbreeding experiments have shown the influence of maturation age of the parents on their offsprings. Hankin *et al.*, (1993) went further by looking at the effect of the sex of the sires on the heritability of age at maturation. They showed that the heritability of age at maturation in females appears to be independent of the age of the male parent. More recently, genetic work has identified the role of a gene (*vgll3*) that may explain up to 40% of the variability in age at maturation in salmon (Barson *et al.*, 2015). This gene has a sex-specific co-dominance and could therefore explain the observed differences in age at maturation between males and females. Recent genetic analyses have shown a decline over time in the frequency of the allele associated with late maturation in Norwegian salmon populations (Czorlich *et al.*, 2018, 2022) in the recent decades. Czorlich et al. (2022) attributed those changes to the combination of a direct fisheries induced evolution, as a response to temporal changes in net fishing pressure in river (selection against early maturation), and indirect fisheries induced evolution as a response to decline in the capelin stocks (one of the main salmon preys at sea) due to overfishing (selection against late maturation).

Predicting evolutionary responses of a trait to selection forces requires accurate estimates of the heritability of the concerned trait. Heritability estimates are based on a decomposition of the variance of the trait into genetic and residual variance (which contains the environmental variance). Two types of heritability are commonly used in the literature: Heritability in the broad sense ($H^2 = V_g/V_p$) which is a ratio between genetic and phenotypic variances and heritability in the narrow sense ($h^2 = V_a/V_p$) a ratio between additive genetic variance and phenotypic variance. Narrow sense heritability is the more useful and easily estimated quantity, and will be simply referred to as heritability. Even if heritability is really well studied for some traits of economically important reared species, the results are rarely extendable to natural population. Indeed, the variances used to calculate heritability differs among populations and even varies over time for the same population, even if expectations exist according the type of traits (Hill, 2013).

Estimating heritability in controlled experiments have been known for a long time (Lande, 1979). Consequently, heritability values for a large number of traits (Hallerman, 2003) are available for numerous agronomic species (animals and plants). Generally, scientists estimate heritability from general pedigrees using linear mixed models and from genomic relatedness

estimated from genetic markers (Dodds *et al.*, 2007). However, these methods are expensive and need controlled environment which is not easy to implement for populations.

Estimating heritability for natural population is even more challenging. In natural population, only the phenotypic variance can generally be observed or measured directly. Then, one simple way to estimate heritability for natural populations is to use simple designs such as the correlation of offspring and parental phenotypes (offspring-parent regression, Hallerman, 2003; Fox and Wolf, 2006) when data are available on both the parents and their progeny. Still, estimating heritability for natural population is thus quite challenging, and examples remains relatively scares. Childs *et al.*, (2016) used a model derived from an integral projection model (IPM) to study egg-laying date evolution in a population of Great tits using individual and pedigree data in an inference perspective. DeFilippo *et al.*, (2019) build an integrated statistical model to infer the dynamics of early males called "jacks" in sockeye salmon (*O. nerka*) using population data (age composition, age class abundance...). They observed an increase in the proportion of jacks, small salmons with low commercial value, impacting the economics of the fishery. Environmental factors could not explain this increase. Instead, they evaluated a strong positive correlation between the proportion of individuals maturing as jacks in the cohort (offsprings) and the proportion of jacks among the spawners (parents), interpreted as a signal of strong heritability of this trait. With a similar purpose, Bromaghin *et al.*, (2011) built a complex model of chinook salmon population dynamics incorporating numerous data including size-selective exploitation, assortative mating, heritability of size and age and more to investigate the potential evolutionary consequences of size-selecting fishing.

Once heritability is estimated, evolutionary change can be predicted using the breeder's equation (Lush., 1937). The breeder's equation relates the change in mean across a generation (the response) to the product of the within-generation change (the selection differential through the life cycle) and a measure of how the character value is transmitted across generation (heritability). For instance, Boëns (2022) has developed an approach (inspired from Swain *et al.*, 2007) to integrate the response to selection for anchovy and sardine using otolith growth data to determine whether declines in size-at-age were due to evolutionary or plastic responses.

This work aims at developing a statistical integrated population model to separate out heritable and plastic response in the age at maturation of Atlantic salmon. The approach builds on an integrated population model for the salmon population of the Scorff river developed by Tréhin *et al.* (in prep.). Our model incorporates quantitative genetics methods traditionally used with individual data (Parent-Offspring regression, Breeder's equation) within this population

dynamic model, drawing inspiration from previous work at the population scales (DeFilippo *et al.,* 2017; Boëns, 2022). First, an offspring-parent relationship is developed within the life cycle to estimate heritability in the salmon age at maturation. Second, to separate out the influence of evolutionary changes and plastic response on the variations of this key life-history trait, the model is complemented by testing the influence of growth during the first summer at sea on the maturation rate. Third, the population model incorporating heritability in the maturation age is used to simulate the response of the population to selective fisheries scenarios.

II.   Material and methods

1. *Study site*

The Scorff river is a 75 km long coastal river draining a 480 km^2 basin located in the South of Brittany in France, and having its estuary in the Bay of Biscay (Figure 1). Since 1994, a migratory fish monitoring station has been set up at the end of the tidal influence zone in Pont Scorff. Fish are trapped throughout the year and particularly during the upstream and downstream migration. The station has been used by INRAE (Institut national de la recherche pour l'agriculture, l'alimentation et l'environnement) since 1995 to collect data on the salmon population of the Scorff. The fish are captured at the smolt stage during their migration to the sea, as well as at the adult stage during their return to reproduce in the river. Each fish captured at the trap has its fork length measured, and a scale sample is taken from the standard area for age determination, molecular sexing, and growth measurement (Baglinière *et al.*, 1985 ; Shearer, 1992). All data and samples are available as part of the COLISA (Collection of ichthyological samples) collection (Marchand *et al.,* 2019). Salmon in the Scorff River typically spend one (1SW) or two (2SW) winters at sea. Individuals spending three winters at sea or spawning more than once represent a very small proportion of returns (≤1% of captures) and will be neglected for our study. In this population, returning adults are dominated by 1SW (83%) with a majority of males among 1SW (54% males) and females among 2SW (84% females).
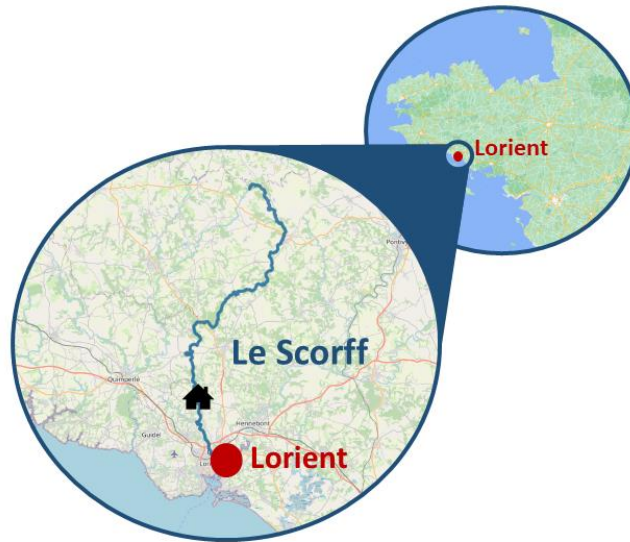
Figure 1: Location of the Scorff river and the monitoring station (black house) in Pont Scorff in Brittany (France).

2. Data

a. *Abundance estimates*

Abundance data were obtained from a model using salmon trapping data at the downstream and upstream ends. A hierarchical Bayesian model accounting for imperfect detection has previously been developed to estimate the probability distribution for the annual abundance of smolts (all ages taken together) and returning adults by sea age class (1SW and 2SW) (Buoro *et al.*, 2019). We fitted our model with abundance estimates of smolt from 1996 to 2020, of 1SW from 1994 to 2019 and of 2SW from 1994 to 2020). Uncertainty in abundance estimates is explicitly accounted for in the model (see below).

b. *Smolt age at migration*

Each year during the smolt migration at sea, smolt are captured and aged using an age-length key to estimate the proportion of smolt of age 1 (smolt 1) and age 2 (smolt 2) migrating at sea. The proportion of smolt 1 varies between 52% and 99% given the 24 years of data (1996-2019).

c. *Sexing*

The sex of A. salmon is genetically determined from birth, but sexual dimorphism is virtually undetectable until spawning. The annual sex ratio of smolts, one-sea-winter adults, and two-sea-winter adults was assessed based on a subsample of approximately 30 smolts and 60 adults per year (30 1SW and 30 2SW). We have data from 1996 to 2018 for smolt and from 1994 to 2020 for adults. DNA extracted from the scales was used to determine the sex of each individual

using a multiplexed sex marker q-PCR protocol for the French data (A.-L. Besnard, personal communication). In total, 2292 individuals were successfully sexed: 639 smolts, 976 1SW adults and 677 2SW adults (Table I).

d. *River catches*

River catches (1SW and 2SW) were also used in this study. These are very well informed and reliable due to the regulations around recreational salmon fishing. These data are available from 1994 to 2020.

e. *Fecundity*

Fecundity was defined as the number of eggs laid per female and was specific for each sea-age. Here, we used data from Nevoux *et al.* (2020) that capture decline of females fecundity over time, based on a length-fecundity relationship and accounting for the decrease in average length of females over time in the Scorff River. No data were available for male 1SW and 2SW, so their relative contributions to the spawning stock were supposed equal.

f. *Growth anomalies*

The growth at sea was assessed from 1996 to 2016 by the analysis of scales of returning adults for a subsample of 30 individuals per year and per stage (1SW, 2SW). Circuli measurements are used as a proxy of body length increment during the marine sojourn (see Tréhin *et al.,* (2021) for further details). The width of the growth increment corresponding to the first summer at sea was used. It covers the period from the river to sea transition to the beginning of the first winter annulus. This variable is then averaged over all individuals and standardized as a growth anomaly over time that will be used as an explanatory variable for the probability of maturation as 1SW in our model considering plastic response to environmental changes.

3. *Bayesian integrated model*

a. Model outlines

We built a stage-structured population model that describes the main demographic transitions from the eggs to the spawners stage over 26 cohorts (Figure 2). The model is composed of three observed stages (smolts, return 1SW and return 2SW) and 7 non-observed latent stages (eggs, parr, surviving post-smolts, maturing post-smolts, non-maturing post-smolt, spawners 1SW, spawners 2SW). Males and females are considered separately from the smolts to the mature adult stages. It is necessary to account for the difference in life-history for males and females,

with females generally maturing later than males and consequently unbalanced sex-ratio in 1SW and 2SW returns compared to smolts.

The model is built in a Bayesian state-space framework (Parent and Rivot, 2013 ; Rivot *et al*, 2004). It incorporates both environmental stochasticity through random variations in demographic transition rates over time, and observation errors in the abundance of smolts and adults and in the proportion of males and females in smolts and adults. The primarily objective of the integrated statistical approach is to estimate two key demographic parameters (together with their variation in time), the survival of post-smolts at sea during the first year at sea before the maturation decision, and the maturation rate. Additional development of the model aims at quantifying how growth during the first summer at sea (plasticity) and heritability can explain the time variation of the maturation rate.
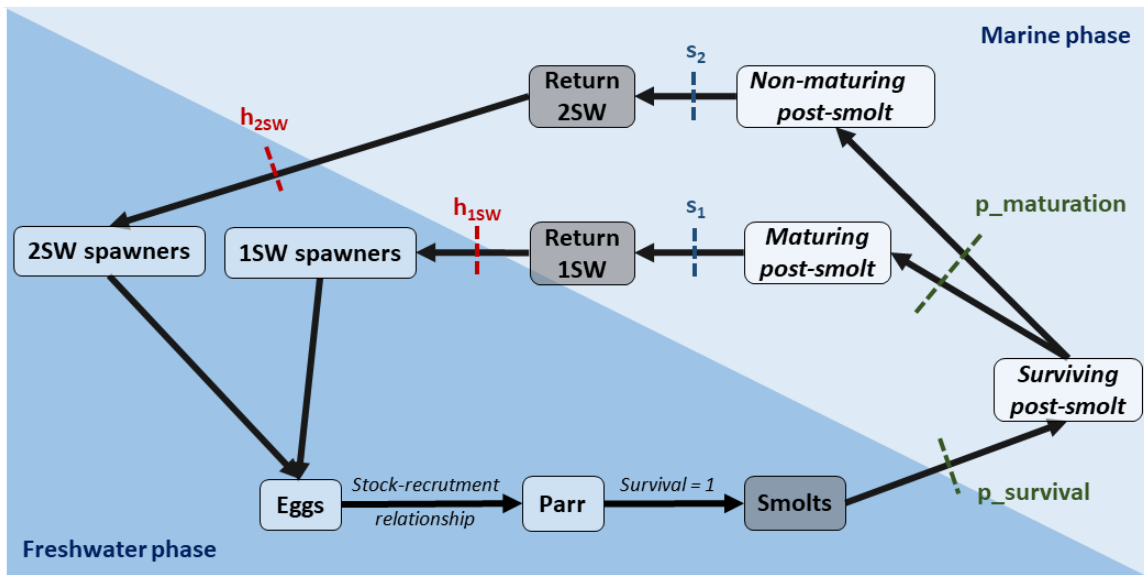
Figure 2: Representation of the stage-structured population model from eggs to spawners. Dark grey boxes are observed sex-specific abundances at smolt, 1SW and 2SW return stages. Light grey boxes represent non-observable life stages, abundance of eggs, parr, surviving post-smolt, maturing and non-maturing post-smolt, 1SW and 2SW spawners. Green dotted lines are estimated transition rates during the first summer at sea: survival (p_survival) and maturation (p_maturation). Blue dotted lines are the fixed survival probabilities after the maturation decision to 1SW (s_1) and 2SW (s_2) returns. Red dotted lines are the exploitation rates in river for 1SW (h_{1SW}) and 2SW (h_{2SW}).

In the following we first present the general structure of the population dynamic model (state-process), before describing the observation model that integrate available data while accounting for observation errors. We then detail the modelling of environmental stochasticity in the

transition rates and the integration of an explanatory variable in the plastic component (growth anomalies) as well as a heritable component for the maturation rate. Finally, we present the estimation of the heritable component for the maturation rate as well as the integration of the breeder's equation to predict response to selection.

b. *General state process for the population model*

The state process uses latent variables to model the changes of abundance from one stage to another over time, in males and females separately. Starting from the number of females spawners 1SW and 2SW at year t denoted $N1SWspawners\,♀_t$ and $N2SWspawners\,♀_t$, the number of eggs $Neggs_t$ is obtained as:

$$Neggs_t = N1SWspawners\,♀_t * f1SW_t + N2SWspawners\,♀_t * f2SW_t \qquad (1)$$

where $f1SW_t$ and $f2SW_t$ are the fecundity (number of eggs per female) of 1SW and 2SW salmons, respectively. Then eggs survive as parr denoted $Nparr_{t+1}$ (young salmon) following a Beverton and Holt density-dependent survival, similarly to the model developed in Lebot *et al.*, (2022) over all Brittany rivers.

$$Nparr_{t+1} = \frac{Neggs_t}{\frac{1}{\alpha} + \frac{Neggs_t}{k}} * e^{\varepsilon_t} \qquad (2)$$

where α is the maximum survival, k is the carrying capacity (maximum number of parr produced) and ε_t considered as iid $\sim$ N(0, $\sigma_{parr}{}^2$) with $\sigma_{parr}{}^2$ the variance of the recruitment process (in log-scale). As the parr-smolt survival rate was arbitrarily set to 1 the stock-recruitment account for all the variability between eggs and smolts. Then smolts that spend one year in freshwater and those that spend two years ($Nsmolts1_{t+2}$ and $Nsmolts2_{t+3}$, respectively) are separated using the smolt age at migration (estimated) $p\_smolt\_cohort_t$, allowing us to follow cohorts in time.

$$Nsmolts1_{t+2} = Nparr_t * p\_smolt\_cohort_t \qquad (3)$$

$$Nsmolts2_{t+3} = Nparr_t * (1 - p\_smolt\_cohort_t) \qquad (4)$$

Smolt migrating year t are the sum of one and two years old smolts migrating year t (but that belong to two different cohort).

$$Nsmolts_t = Nsmolt1_t + Nsmolt2_t \qquad (5)$$

Then the life cycle become sex-specific by separating males and females ($Nsmolts_{t,male}$ and $Nsmolts_{t,female}$, respectively) using the proportion of female (estimated) in smolt at year t, $prop\_female\_smolt_t$.

$$Nsmolts_{t,female} = Nsmolts_t * prop\_female\_smolt_t \tag{6}$$

$$Nsmolts_{t,male} = Nsmolts_t * (1 - prop\_female\_smolt_t) \tag{7}$$

The number of surviving post-smolt, denoted $Nsurvivors_{t,sex}$ is obtained from migrating smolts $Nsmolts_{t,sex}$ as:

$$Nsurvivors_{t+1,sex} = Nsmolts_{t,sex} * p\_survival_t \tag{8}$$

where $p\_survival_t$ is the survival rate during the first summer at sea (estimated), assumed equal between males and females. This parameter has been estimated supposing random variations among years around an average v with random variations γ_t considered as iid ~N(0, σ_{surv}^2):

$$logit(p\_survival_t) = v + \gamma_t \tag{9}$$

Post-smolts can mature (and potentially return to the river as 1SW), with a maturation rate denoted $p\_maturation_{t,sex}$ (estimated), that is specific to males and females (Tréhin, 2021). Fish that do not mature at that time delay maturation before returning to the river as 2SW fish upon survival, with the rate $1 - p\_maturation_{t,sex}$:

$$Nmature_{t,sex} = Nsurvivors_{t,sex} * p\_maturation_{t,sex} \tag{10}$$

$$Nnonmature_{t,sex} = Nsurvivors_{t,sex} * (1 - p\_maturation_{t,sex}) \tag{11}$$

with $Nmature_{t,sex}$ and $Nnonmature_{t,sex}$ the sex-specific abundances of maturing and non-maturing fish at the end of first summer at sea. Different models for the variation of the maturation rate (including the influence of growth and/or a heritable component) will be detailed in the following.

Before returning in freshwater, fish suffer additional mortality rate, denoted s_1 and s_2 for 1SW and 2SW respectively (fixed):

$$N1SW_{t,sex} = Nmature_{t,sex} * s_1 \tag{12}$$

$$N2SW_{t+1,sex} = Nnonmature_{t,sex} * s_2 \tag{13}$$

where $N1SW_{t,sex}$ and $N2SW_{t,sex}$ are the sex-specific abundances of 1SW and 2SW returns. Survival rates s_1 and s_2 are fixed values considered constant over time and equal between sexes. Following life cycle models developed by ICES (Olmos *et al.*, 2019), s_1 and s_2 are directly calculated from a fixed monthly mortality rate (M is considered equal for 1SW and 2SW and for males and females, fixed to 0.03 month^{-1}), and Δt_{1SW} and Δt_{2SW} the number of additional months at sea after the maturation decision for 1SW and 2SW, respectively:

$$s_1 = e^{-M * \Delta t_{1SW}} \tag{14}$$

$$s_2 = e^{-M * \Delta t_{2SW}} \tag{15}$$

Following the hypotheses that maturation decision is taken in autumn of the first year at sea (November, Tréhin *et al.*, in prep.) and that 1SW fish return on average in July while 2SW fish stay an additional year and return in March of the following year, we fixed $\Delta t_{1SW} = 9$ and $\Delta t_{2SW} = 17$. These differences in timing generates a +27% differential in survival from the maturation decision to the return for 1SW with regards to 2SW ($s_1 = 0.76$ and $s_2 = 0.60$).

In the river and before the reproduction the salmons are exposed to fishing, with exploitation rates denoted $h1SW_t$ and $h2SW_t$ (estimated) for 1SW and 2SW respectively:

$$N1SWspawners_{t,sex} = N1SW_{t,sex} * (1 - h1SW_t) \tag{16}$$

$$N2SWspawners_{t,sex} = N2SW_{t,sex} * (1 - h2SW_t) \tag{17}$$

where $N1SWspawners_{t,sex}$ and $N2SWspawners_{t,sex}$ are the sex-specific abundances of 1SW and 2SW that are able to reproduce.

c. *Observation equations*

The model is fitted to abundance data at the smolt and adult stages, and completed by observation equations on the sex-ratio (smolts and adults), freshwater catches (adults), and smolt age at migration.

Abundance data were available as log-normal distributions estimated by a separate model (Buoro *et al,.* 2019). Those distribution were used to approximate likelihoods in the state-space model, following the pseudo-likelihood method (Michielsens *et al.*, 2008 ; Olmos *et al.*, 2019).

For any year *t* the expected mean of the distribution derived from the observations models for smolts (respectively 1SW and 2SW) in log scale, denoted $E_{\log (Nsmolt_t)}$ (respectively $E_{\log (N1SW_t)}$ and $E_{\log (N2SW_t)}$), is considered as an observed realization of a normal distribution of non-observed smolt abundance (in log-scale) $\log(Nsmolt_t)$ (respectively $\log(N1SW_t)$ and

log($N2SW_t$)) with known variance $\sigma^2_{smolt_t}$ (respectively $\sigma^2_{1SW_t}$ and $\sigma^2_{2SW_t}$) set to the value derived from the observation error models. These observation errors are considered independent across years and stages.

$$E_{\log(Nsmolt_t)} \sim Normal\ (\log(Nsmolt_t),\ \sigma^2_{smolt_t}) \tag{18}$$

$$E_{\log(N1SW_t)} \sim Normal\ (\log(N1SW_t),\ \sigma^2_{1SW_t}) \tag{19}$$

$$E_{\log(N2SW_t)} \sim Normal\ (\log(N2SW_t),\ \sigma^2_{2SW_t}) \tag{20}$$

Observation models to integrate data on sex-ratio for smolts and adults have also been used. The number of individuals sexed as females and males among scales samples for smolts and adults were considered following a hypergeometric distribution with males/females proportion derived from the state process of our model:

$$Sex-ratio_{smolt\,♀_t} \sim Hypergeometric\ (Nsmolt\,♀_t, Nsmolt\,♂_t, Nsample\_smolt_t) \tag{21}$$

$$Sex-ratio_{1SW\,♀_t} \sim Hypergeometric\ (N1SW\,♀_t, N1SW\,♂_t, Nsample\_1SW_t) \tag{22}$$

$$Sex-ratio_{2SW\,♀_t} \sim Hypergeometric\ (N2SW\,♀_t, N2SW\,♂_t, Nsample\_2SW_t) \tag{23}$$

where $Nsample\_smolt_t$ (respectively $Nsample\_1SW_t$ and $Nsample\_2SW_t$) are the number of smolts (respectively 1SW and 2SW) genetically sexed. $Nsmolt\,♀_t$ and $Nsmolt\,♂_t$ (respectively $N1SW\,♀_t, N1SW\,♂_t$ and $N2SW\,♀_t, N2SW\,♂_t$) are the number of smolts (respectively 1SW and 2SW) in the state process. In opposition to the simpler binomial distribution, hypergeometric distribution assumes a finite population size. As sample size was sometimes close to population size, this assumption was important, especially for 2SW.

Observation equation for the smolt proportion at age has been developed to complete the abundances and sex-ratio equations. The proportion of smolt 1 (and smolt 2) migrating at year t, denoted $prop\_smolt_{migr_t}[1]$ (and $prop\_smolt_{migr_t}[2]$) derived from the state process by (eq. 24) was fitted to the data following a Dirichlet distribution:

$$prop\_smolt_{migr_t}[1,2] = [\frac{Nsmolt1_t}{Nsmolt_t}, \frac{Nsmolt2_t}{Nsmolt_t}] \tag{24}$$

$$prop\_smolt_{data_t}[1,2] \sim Dirichlet\ (prop\_smolt_{migr_t}[1,2] * Nsample_t) \tag{25}$$

where $prop\_smolt_{data_t}[1,2]$ are the proportion of smolts 1 (and smolt 2) determined from observation and $Nsample_t$ an arbitrary high number, as the estimation of smolt age proportion are considered highly accurate (Buoro, Prévost, pers. comm.).

An observation model has also been used to integrate data on freshwater catches of 1SW and 2SW salmons. For any year t the expected mean of the catches distribution in log scale, denoted $E_{\log(catches\_1SW_t)}$ ($E_{\log(catches\_2SW_t)}$), is considered as an observed normal distribution of catches (in log-scale) $\log(catches_{1SW_t})$ ($\log(catches_{2SW_t})$) with known variance $\sigma^2_{catches\_1SW_t}$ ($\sigma^2_{catches\_2SW_t}$) set to 0.05, a relatively small value to account for the high reliability of catches data.

$$E_{\log(catches\_1SW_t)} \sim Normal\ (\log(catches_{1SW_t}), \sigma^2_{catches_{1SW_t}}) \tag{26}$$

$$E_{\log(catches\_2SW_t)} \sim Normal\ (\log(catches_{2SW_t}), \sigma^2_{catches_{2SW_t}}) \tag{27}$$

d. *Alternative models for the maturation rate*

Baseline model

The baseline model supposes random variations among years in maturation rates around a grand mean (denoted μ, estimated) common between sex but also a sex-specific term (α_{sex} ; estimated) to account for differences in mean maturation rate between sexes (Tréhin *et al*., 2021; Tréhin *et al*., in prep.). Additionally, sex-specific random components $\varepsilon_{t,sex}$ represent the unexplained variability, considered as iid ~N(0,$\sigma_{mat,sex}$²) with sex-specific variance. An additional effect of smolt age on maturation rate was also tested but its estimation was not considered robust enough to be further considered (Appendix I).

$$logit(p\_maturation_{t,sex}) = μ + \alpha_{sex} + \varepsilon_{t,sex} \tag{28}$$

Integrating an explanatory variable for the plastic response

Similarly to Tréhin *et al*. (in prep), the inter-annual variation of the average growth during the first summer at sea was added as an explanatory variable to capture part of the annual variation of the maturation rate (plastic response):

$$logit(p\_maturation_{t,sex}) = μ + \alpha_{sex} + β_{sex} * growth_t + \varepsilon_{t,sex} \tag{29}$$

where $growth_t$ denote the time series of growth anomalies (data) for smolt year t (common for males and females) and $β_{sex}$ the slopes of the regression in the logit scale that depend on sex. Sex-specific slopes $β_{sex}$ and residual variations $\varepsilon_{t,sex}$ (iid ~N(0, $\sigma_{mat,sex}$²) with sex-specific variance) were necessary to avoid stronger effect in females compared to males due to the higher maturation rate for males and the distortion of the logit scale for values close to one.

In addition, we quantify how much variation in maturation rate is explained by growth anomalies by calculating the amount of residual variance captured by the covariate as:

$$Explained\ variance = \frac{\sigma_{res}^2(NoCov) - \sigma_{res}^2(Cov)}{\sigma_{res}^2(NoCov)} \qquad (30)$$

where $\sigma_{res}^2(Cov)$ and $\sigma_{res}^2(NoCov)$ are residual variances obtained from the models with and without covariates, respectively. Residual variance is calculated as $\sigma_{mat,sex}{}^2$.

Integrating the heritable component into the maturation rate

A parent-offspring regression approach (Walsh and Lynch, 2018, chapter 13) was used to estimate heritability. This approach is appropriate to our framework as it does not require genotypic data but only variations of abundance for the different phenotypes. In its general form, the parent-offspring regression is written as:

$$Y = (1 - h^2)\mu + h^2 X \qquad (31)$$

with Y the mean value of the offspring's trait, X the mean value of the parent trait, μ the mean value of the population and h^2 the narrow sense heritability.

Following this general concept, specific equations were implemented in our model to accommodate for the specificities in salmon life histories and the difference in trait for both sexes:

$$logit(p\_maturation_{\ t,sex}) = \qquad (32)$$

$$\mu + \alpha_{sex} + h^2 * midparent_{sex,cohort} + \varepsilon_{t,sex}$$

with *t* denoting the smolt migration year, and *cohort* being *t-3* for smolt 1 and *t-4* for smolt 2 as those fish don't have the same parents. Those time lags are needed to accommodate the variability in smolt ages. Indeed, a salmon parr can spend one or two year in freshwater before migrating as smolt. Consequently, if the maturation rate is partially heritable, the maturation rate of a smolt 1 migrating year *t* may depend upon the phenotypes of the spawners reproducing year *t-3*, and the maturation rate of a smolt 2 migrating year *t* may depend upon the phenotypes of the spawners reproducing year *t-4* (Figure 3). Two parent-offspring regression, one for each offspring sex were built to accommodate for the mean differences between sexes (see Appendix II for details). A sex effect α_{sex} accommodates for the mean differences between sexes as in the baseline model. Note however that one unique heritability parameter h^2 common for males and females is considered.

Also, as advocated for sex-specific parent-offspring regressions (Walsh and Lynch, 2018, chapter 13), the parent trait is expressed as a mid-parent trait averaged over the two sexes. Note however that this mid parameter trait was standardized differently for males and females regressions (hence the subscript sex on $midparent_{sex,cohort}$) to accommodate for the differences in average level of the maturation rate in the natural scale (see Appendix II for a detailed justification of its calculation). Last, an additional random term $\varepsilon_{t,sex}$ (iid ~ N(0, $\sigma_{mat,sex}^2$) with sex-specific variance) is incorporated to capture the residual variation of the trait not captured by the heritable component. The amount of residual variance captured by the mid-parent trait covariate (hence captured by heritability) is calculated using an approach similar to eq. (30).
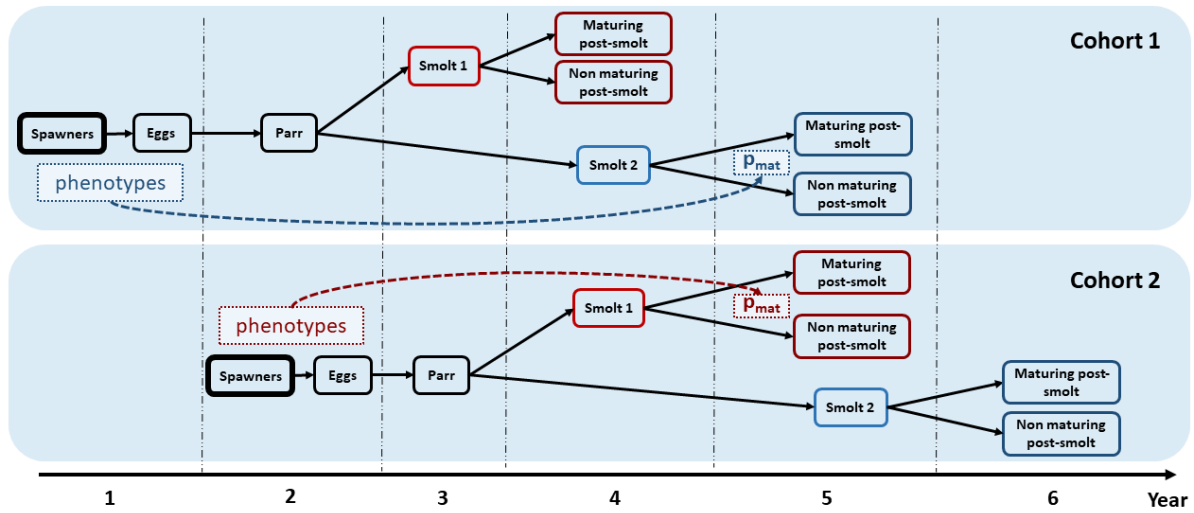
Figure 3: Diagram representing the mixing in the cohorts for a given year. For example, in year four, smolts migrating are not from the same spawners. Smolts 1 are from spawners at t-3 and smolt 2 are from spawners at t-4.

Combining the influence of growth and heritability

To quantify the relative contribution of the plastic response (influence of growth at sea) and of heritability on the time variation of the maturation rate, we combined equations 29 and 32:

$$logit(p\_maturation_{t,sex}) \tag{33}$$

$$= \mu + \alpha_{sex} + h^2 * midparent_{sex,cohort} + \beta_{sex} * growth_t + \varepsilon_{t,sex}$$

Estimating heritability using the breeder's equation

Parent-offspring regressions are useful methods for detecting and estimating heritability but cannot be used to predict response to selection. To that aim, simplification of the Price equation

lead to the ready-to-use and long-standing breeder's equation (Lush, 1937 ; Price, 1970 ; Walsh and Lynch, 2018):

$$R = h^2 S \qquad (34)$$

with R the response to selection expressed as the mean traits difference between successive generations and S the selection differential that is the difference between the population mean trait before and after selection.

Hence in the perspective of parameterizing a population model to simulate the response to selection, heritability was also estimated using the Breeder's equation adapted in our model to accommodate for a sex-specific trait, using midparent traits calculated before and after selection during the marine phase (that is just after the maturation of post-smolt and at the spawner stages), denoted $midparent_{before_{t,sex,cohort}}$ and $midparent_{after_{t,sex,cohort}}$, respectively (eq 35, see appendix II):

$$logit(p\_maturation_{t,sex}) = midparent_{before_{sex,cohort}} +$$
$$h^2 * (midparent_{after_{sex,cohort}} - midparent_{before_{sex,cohort}}) + \varepsilon_{t,sex} \qquad (35)$$

e. *Prior distributions*

Weakly informative priors are set on almost all parameters and state variables that are not defined by a demographic transition (Appendix IV). To estimate the heritability parameter (h^2) in the offspring-parent relationship and in the breeder's equation different priors were tested to assess prior influence on the posterior distribution.

f. *MCMC simulations*

Bayesian posterior distributions are estimated using Markov chain Monte Carlo (MCMC) methods using the R Nimble package (https://r-nimble.org; from de Valpine *et al.*, 2017). Each model is run with 10 independent chains of 10 million iterations. The first 2 million iterations are discarded as a burn-in period. Then, one iteration every 10 000 is sampled to estimate the posterior distribution of each parameter. This gives us 800 iterations for each chain, that is a total of 8000 posterior samples. We check convergence for all parameters with a Gelman-Rubin test (Rhat statistic <1.05 ; Gelman and Rubin, 1992) and by achieving an appropriate effective sample size (>1000). The goodness of fit of the model to the different data sources is analyzed by plotting the observation error distribution against the posterior distribution of the

corresponding state variable. Convergence and fit assessment results are available in appendix V and VI.

4. *Using the model to simulate the response to selection*

The life cycle model, including heritability as estimated from the Breeder's equation, was then used to simulate the response to selective fisheries. Simulations were done using the same model while incorporating both process uncertainty and uncertainty around parameters estimates.

Simulations were done directly within R under several scenarios based on the selection differential between 1SW and 2SW for males and females separately. Selection differential is defined as the ratio of the different selection pressures (exploitation rate, survival rate) combined with the fecundity differential experienced by 1SW and 2SW salmon during their life cycle (between the post-smolt and the spawners stages) (e.q 36 and 37). Note that difference in fecundity were only considered for females (difference in the number of eggs spawned). We considered 1SW and 2SW males have the same fecundity. If this ratio is above 1, 1SW salmon have a higher fitness and if it is under 1, 2SW salmon have a higher fitness.

$$Selection\ differential\ ♀ = \frac{(1 - h1SW) * s_1 * f1SW}{(1 - h2SW) * s_2 * f2SW} \tag{36}$$

$$Selection\ differential\ ♂ = \frac{(1 - h1SW) * s_1}{(1 - h2SW) * s_2} \tag{37}$$

The model was run under 8 scenarios (Table II) defined by different values of the exploitation rate of 1SW ($h1SW$) and 2SW ($h2SW$)) were that control the selection differential. The first scenario is based on averaged values of exploitation rates estimated from the data (see appendix III). Scenario 2 mimics a management strategy with similar exploitation rate between 1SW and 2SW. The last 6 scenarios have been built to cover a maximum range selection differential between 1SW and 2SW while remaining realistic.

The simulation model was then used as an empirical method to derive trait values at evolutionary equilibrium by simulating over 1000 years for each scenario. The short-term response to the selection was investigated looking at the first 15 years of the simulations.

Table 1: Configuration of the different scenarios integrating the exploitation rates of 1SW and 2SW and simulated on 1000 years.

Scenarios	Exploitation rate 1SW ($h1SW$)	Exploitation rate 2SW ($h2SW$)
1	0.067	0.123
2	0.085	0.085
3	0.060	0.160
4	0.060	0.300
5	0.060	0.500
6	0.100	0.060
7	0.300	0.060
8	0.500	0.060

III.   Results

1.   Temporal variability and sex effect on maturation rate

Maturation rate averaged over males and females (Figure 4A) vary over time with a peak of 90% in 2002, a minimum of 65% in 2008 and a mean of 80% on the full time series (1998-2019). Sex-specific maturation rate (Figure 4B) is higher for males than females but exhibit the same decline in 2008. The maturation rate is on average 68% for females and 93% for males and varies between 58% - 83% for females and between 76% - 99% for males. These differences are consistent with Tréhin's *et al.* (in prep) estimations.

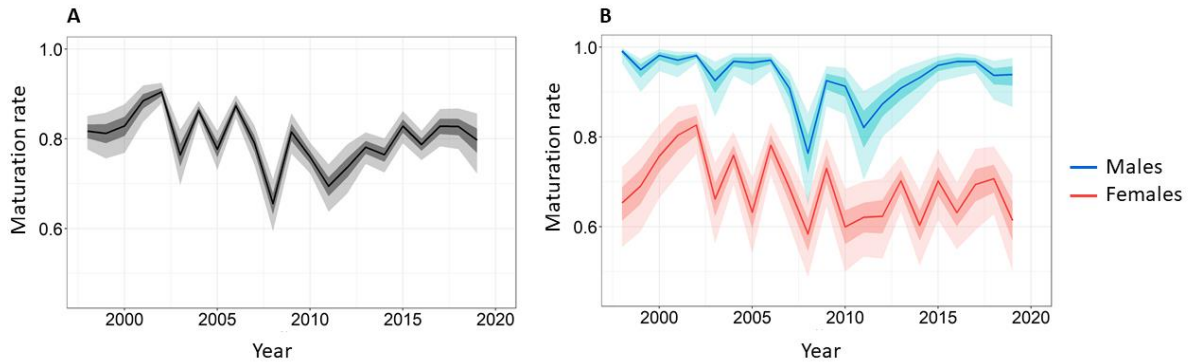*Figure 4: Temporal fluctuations for the common (A) and sex-specific (B) maturation rate. Solid lines with shaded areas represent the median, the 50% and the 90% credibility interval of the posterior distribution of the maturation rate.*

Variations of the maturation rate are weakly synchronous between males and females, but stronger for females in the natural scale. However, because of the distortion of values close to

1 in the logit-scale, the total inter-annual variance ($\sigma^2_{mat,sex}$) is much higher for males (1.00) than for females (0.13).

2. *Estimating heritability using offspring-parent regression*

Heritability (h^2) has been estimated using the offspring-parent regression in the stage structured model. Despite different priors (Figure 5B), all posterior distributions are relatively similar with a posterior mode around 0.25 (Figure 5A), indicating a strong signal of heritability in the data, ensuring a consistent updating of the prior distribution. Small differences are still observed between the different posteriors. Median values of posterior distribution of h^2 are respectively 0.19, 0.23 and 0.26 for the beta (1, 4), the beta (3, 9) and the uniform (0, 1) prior distributions.
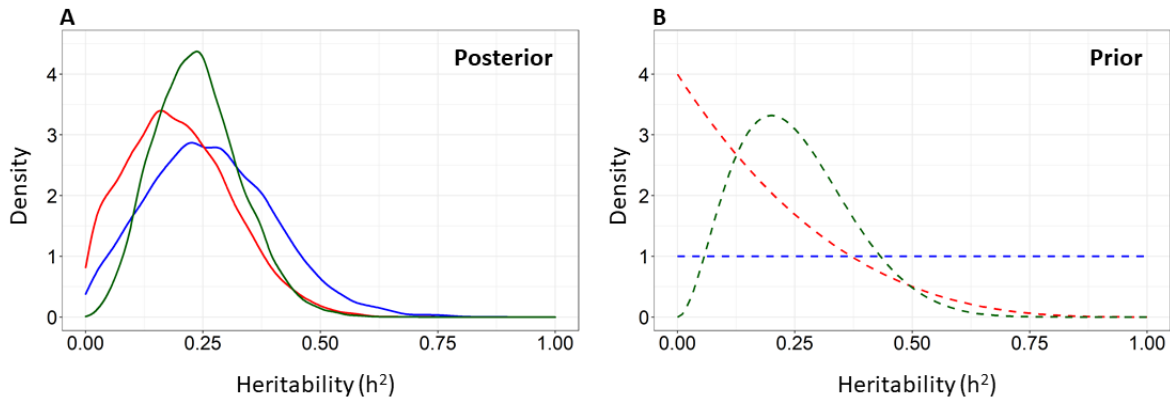
Figure 5: Priors (B) and associated posteriors (A) distributions of the heritability parameter from offspring-parent regression. Blue prior has a uniform distribution (0,1), the red one has a beta distribution (1,4) and the green one has a beta distribution (3,9).

The variation of the males and females maturation rates as a function of the midparent trait (1SW proportion in spawners) illustrates the influence of heritability on the maturation rate at the population scale (Figure 6). This relation is linear in the logit scale and slightly non-linear in natural scale.

Over the whole range of midparent trait, higher variation in the maturation rate (in the natural probability scale) is observed for females than for males. Model predicts that the maturation rates can increase from 92% to 97% for males and from 62% to 88% for females for a midparent trait that increase from 83% to 99% for males and from 38% to 76% for females, respectively (posterior median values).
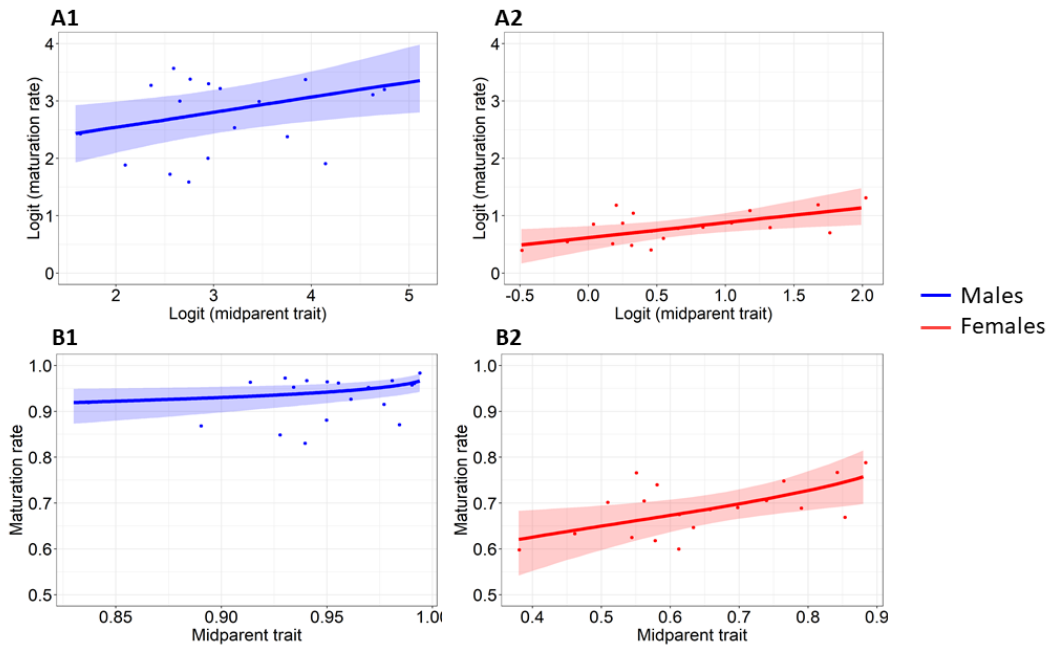
Figure 6: Variation of maturation rate as a function of midparent trait in the logit (A) and natural (B) scale, for males (blue) and females (red). Solid lines with shaded area represent the median and the 95% credibility interval of the marginal posterior distribution of the maturation rate. Points represent marginal posterior distribution of maturation rates estimated for each year. To build these curves, a heritability value of 0.26 (median of posterior value of h^2 using the uniform prior) has been used.

Comparison of the residual variance of the temporal variations of the maturation rate obtained with or without heritability (h^2 fixed to 0) revealed that heritability explained 17% and 11% of the total variance of the trait for females and males, respectively (those results are obtained using an informative prior for h^2) (Figure 7).
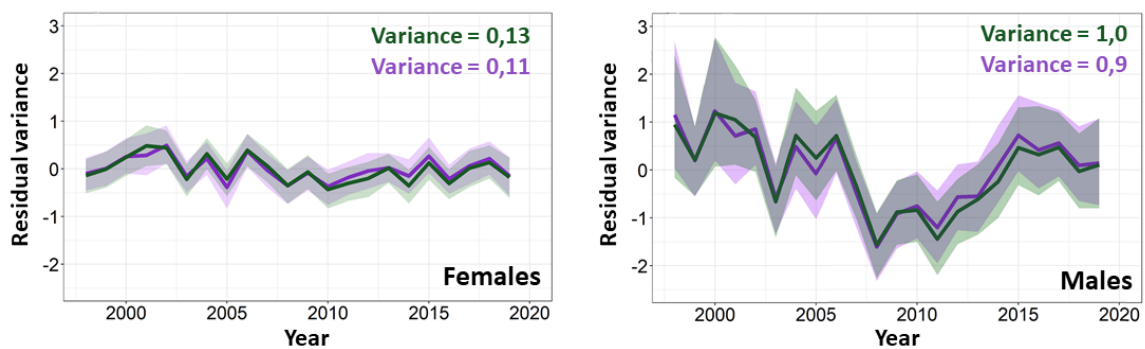
Figure 7: Residual variations in the probability of maturation (interpreted as environmental variations) with (purple curve) and without (green curve) the heritable component for males and females separately. Solid lines with shaded area represent the median and the 95% credibility interval of the marginal posterior distribution of the residual variations.

3. *Quantifying the influence of growth (plastic response) and heritability*

Those analyses were carried out using a default uniform prior on the h² parameter. In a model considering only the influence of growth during the first summer at sea (no heritability) to explain the time variation of the maturation rate, the growth variations capture 25% and 47% of the among year variations in the maturation rate for females and males respectively. This is far larger than the explained variance by the heritable component, especially for males.

Slopes in the logit scales are different between males and females, however, because of the different intercept between sexes, the same variation of growth anomalies leads to similar variation of the maturation rate in the natural probability scale (Figure 8). Model predicts that the maturation rates can increase from 89% to 98% for males and from 64% to 74% for females for a summer growth that increases from 1.60 mm (anomaly = -0.56) to 1.75 mm (anomaly = 0.75).
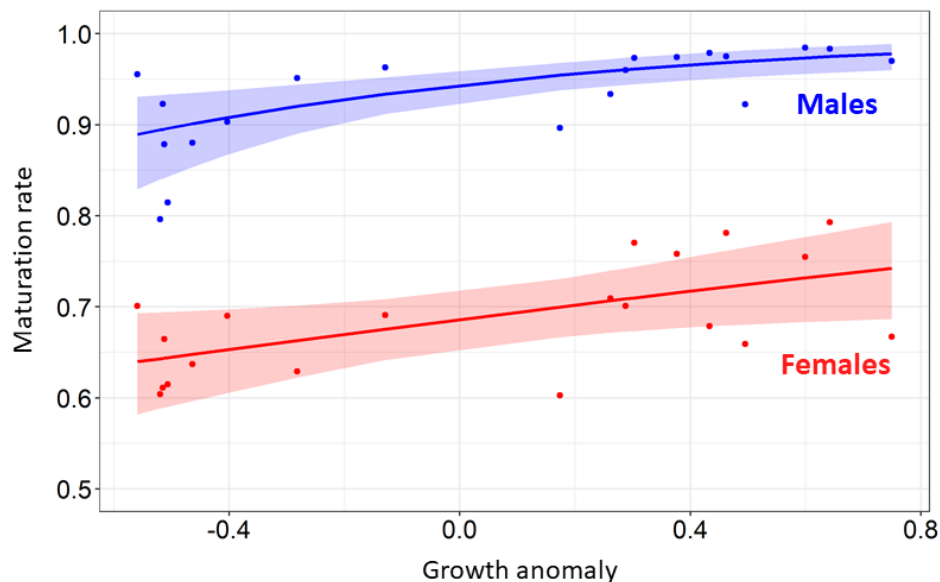
Figure 8: Relationship between maturation rate and the growth anomaly during the first summer at sea. Solid lines with shaded area represent the median and the 95% credibility interval of the marginal posterior distribution of the maturation rate. Points represent marginal posterior distribution of maturation rate for each year.

When both the influence of growth (plastic response) and heritability is considered in the model, estimation of heritability parameters h² falls close to 0 (Figure 9). This indicates a possible confusion between the heritability of the probability of maturation and the effect of growth anomaly.
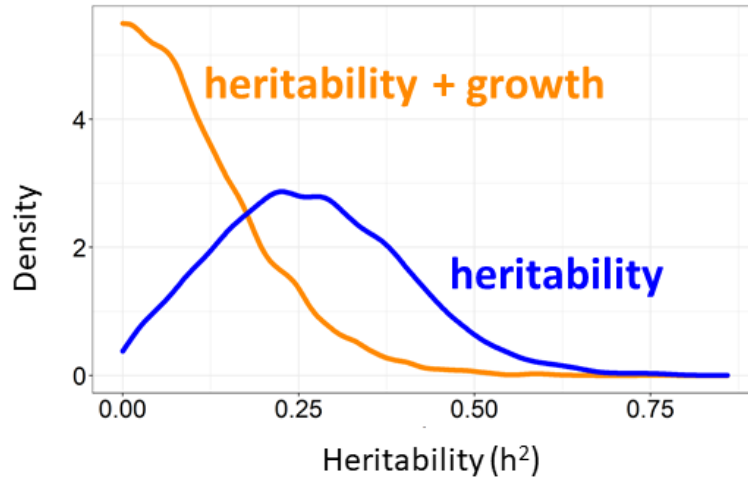
Figure 9: Posterior distributions of the heritability parameter from offspring-parent regression with and without the environmental proxy (growth anomaly). The two posteriors have the same prior, a uniform distribution between 0 and 1.

5. *Estimating heritability using the breeder's equation*

By contrast with the offspring-parent regression, posterior distributions are highly similar to their respective priors in all case (figure 10). This suggest that there is only weak information in the data to infer heritability using the breeder's equation.
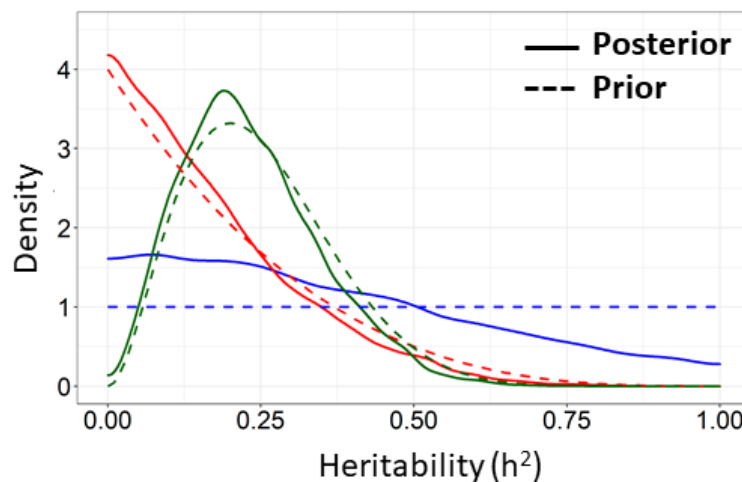
Figure 10: Prior (dotted lines) and associated posterior (solid lines) distributions of the heritability parameter estimated using the breeder's equation. Blue prior is a uniform distribution (0,1), red one is a beta distribution (1,4) and green one is a beta distribution (3,9).

6. *Predicting the response to selection*

Because the literature support the existence of a strong heritability for the maturation rate (Barson et al., 2015 ; Czorlich et al., 2018 ; Gjerde, 1984), the choice was made to run all

simulations using the results obtained with an informative beta distribution (3, 9) on h^2 (Figure 10)

a. Selection differential

Theoretical response surfaces directly derived from equation 36 and 37 (for females and males, respectively) show that males and females have different selection differential (Figure 11).

In the first scenario of exploitation rates (red point), it is more advantageous to be a 1SW for males (selection differential of 1.36 for males) while it is more advantageous to be a 2SW for females (selection differential of 0.81 for females). These differences are explained by the difference of fecundity between 1SW and 2SW females, while 1SW and 2SW males were assumed to have the same contribution to the spawning stock.

Figure 11: Theoretical surface response for differential selection as functions of exploitation rates of 1SW and 2SW salmons for females (A) and males (B). Point represent scenario based on estimated exploitation rates. A value of 1 (black solid line) means that the selection potential is the same for 1SW and 2SW salmons. In other words, there is no advantage to be 1SW or 2SW. On the other hand, a differential selection above 1 means that it is more advantageous to be a 1SW salmon and a differential selection below 1 means that it is more advantageous to be a 2SW salmon.

Using these sex-specific surface responses it is possible to define three different areas, summarizing selection differential for males and females obtained for different combination of 1SW and 2SW harvest rates and predicting the associated evolutionary equilibrium for the trait (1SW only, 2SW only or mixed phenotypes, Figure 12). Additional scenarios cover the different areas: two scenarios (7 and 8) fall in the 1SW area, two (4 and 5) in the 2SW area and three (2, 3 and 6) in the mixed area. We can formulate the following expectations: scenarios falling in the 1SW area will converge to a maturation rate of 1 (which means that all the fish mature the

first year) at a more or less rapid rate depending of the 2SW exploitation rate; scenarios in the 2SW area will converge to a maturation rate of 0 (which means that all the fish mature after two years at sea) at a more or less rapid rate depending of the 1SW exploitation rate; scenarios in the mixed area to converge to an intermediate maturation rate as the selection differential is different between males and females.
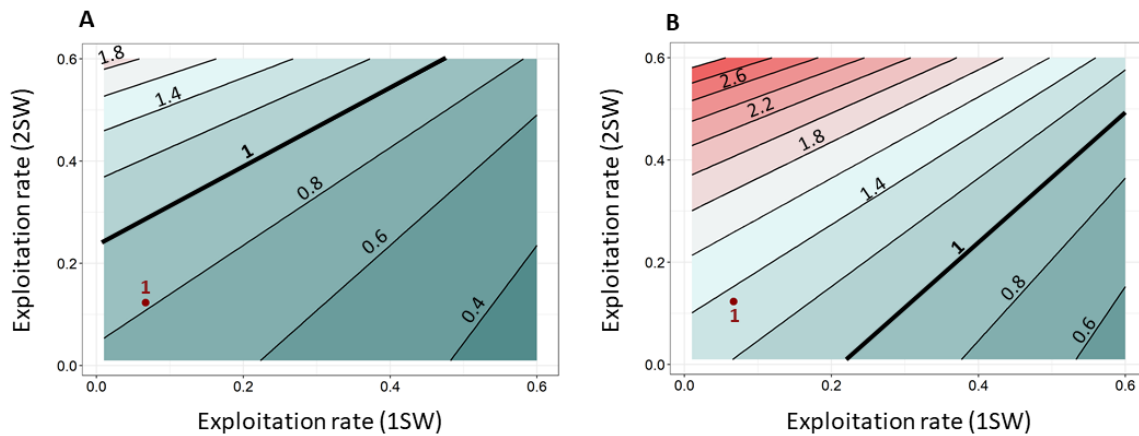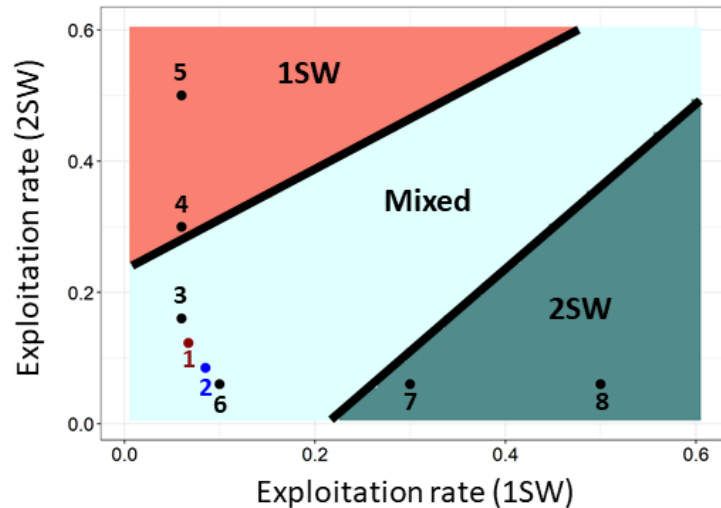

Figure 12: Theoretical surface response for differential selection as functions of exploitation rates of 1SW and 2SW salmons. Points represent the different scenarios considered. Red area corresponds to a differential selection favoring 1SW (males and females) and dark blue area corresponds to a differential selection favoring 2SW (males and females). Light blue area corresponds to a differential selection favoring males 1SW and females 2SW.

b. Predicting trait at equilibrium

Equilibrium (or near equilibrium obtained after 1000 years) follows our expectations (Figure 13): scenarios 4 and 5 converge towards 100% 1SW, scenarios 7 and 8 towards 100% 2SW, and all other scenarios converge toward mixed equilibrium. Scenario 1 (status quo) converged to a relatively high proportion of 1SW compared to historically observed proportion (Figure 13). Scenario 2, with a balanced exploitation rate for both sea age converged to a proportion of 1SW of 50% (Figure 13). Interestingly the last two scenarios converged towards very high (Figure 13, scenario 4) or relatively low (Figure 13, scenario 7) proportion of 1SW, despite their relative proximity in differential selection (Figure 12). Credibility interval are represented in appendix VIII for each scenario and populations size for both 1SW and 2SW in appendix X).
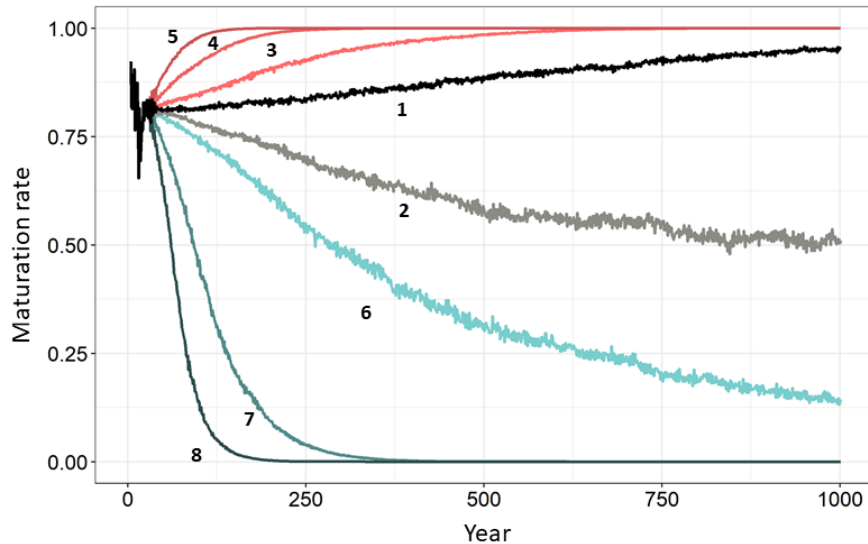
Figure 13: Comparison of the simulations of joint maturation rate on 1000 years based on the different scenarios of exploitation rate.

c. Predicting short-term response to selection

Over 15 years, the short term trends toward evolutionary equilibrium can be identified for all scenario (Figure 14). Interestingly, for all scenarios, the average trend observed in the first 15 years is limited due to the very high environmental stochasticity (see Figure 15 for scenario 1 and Appendix IX for other scenarios). The minimum (65%) and the maximum (92%) maturation rates observed in the hindcast period are more extreme than the minimum (72%) and the maximum (86%) average maturation rates observed in the 15 years forecast period. However, the 90% credibility interval is quite large (Figure 15) and maturation rates after 15 years ranges between 54% and 94% which is outside the range of observed values during hindcast.
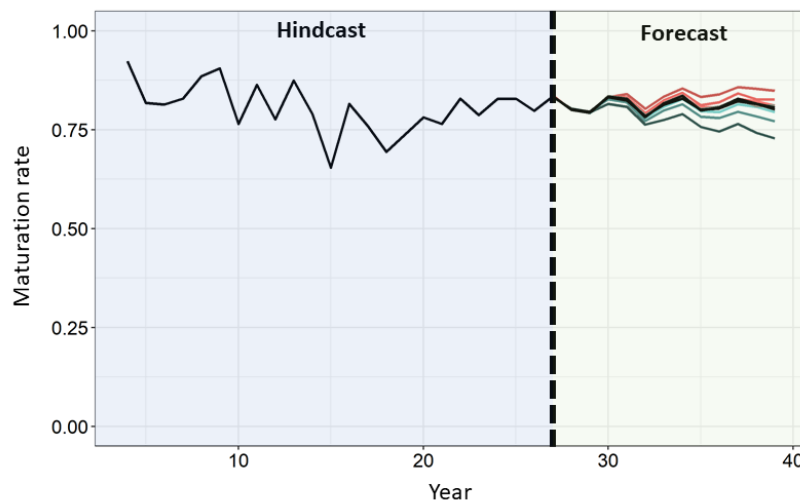
Figure 14: Temporal fluctuation for the hindcasted and forecasted maturation rate for each scenario. Solid line represents the median of the posterior distribution of the maturation rate. Blue area corresponds to the 27 years of hindcast and green areas to the 15 simulated years.
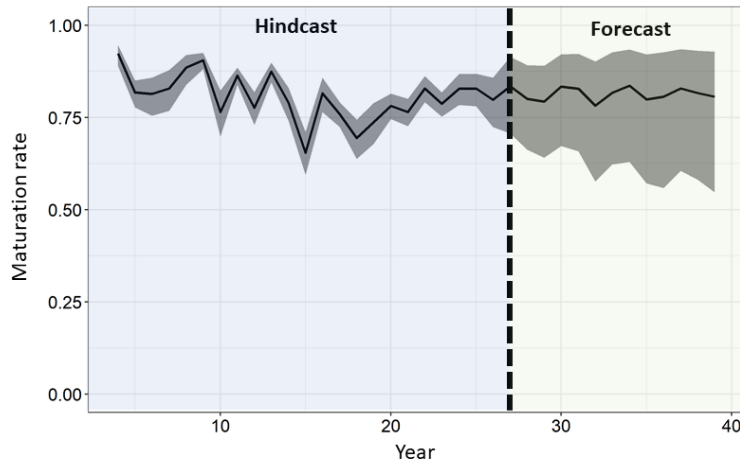
Figure 15: Temporal fluctuation for the hindcasted and forecasted maturation rate. Solid line with shaded area represents the median and the 90% credibility interval of the posterior distribution of the maturation rate.

IV. Discussion

In this study we built on the model developed by Tréhin et al. (in prep.) to develop an integrated stage and sex-structured population model for Atlantic salmon population of the Scorff river (Morbihan, France) describing the main demographic transitions from eggs to adults over 26 cohorts. The model is embedded within a bayesian statistical framework to estimate abundance and key demographic transition rates. The main contribution consists in developing a method to estimate heritability of the maturation rate of salmon after their first year at sea. Relying on the detailed representation of salmon cohorts through their life cycle, we embedded an original sex-specific parent-offspring regression model within the stage-based population model to estimate heritability of the maturation rate. Results demonstrated a heritable signal in this key life-history. Although well detected, the heritability signals explain only a small part of the total variance of this trait, Additionally, another huge contribution of our methodological framework is to explore the possibility to combine modelling of heritability with a plastic component in order to separate out those two signals, a very challenging subject in evolutionary ecology (Crozier *et al.*, 2008 ; Gienapp *et al.*, 2008 ; Réale *et al.*, 2003). Tréhin et al. (2021) and Tréhin et al. (in prep.) already evidenced a positive influence of growth during the first summer at sea

on the maturation rate, and interpret this relation as a plastic response. However, our results show that when combining both the influence of growth (plastic response) and heritability in our model, heritability parameter is estimated close to zero. This result highlights a potential confusion between the heritable signal and the growth anomaly. Last In order to predict response to selection, we adapted the breeder's equation for a sex-specific trait within the population model. The model could predict both evolutionary equilibrium and short-term response to selection under several fishing scenario targeting differentially 1SW and 2SW. Evolutionary equilibrium were consistent with our expectation and appeared quite sensitive to the exploitation rates. Short-term response to selection were largely dominated by the environmental variability highlighting the need for a better understanding of the complex mechanisms that control the variation of maturation rates.

1. *A framework to integrate heritability of a key life-history trait within stage-based population models*

Heritability of key life history traits is rarely considered in fish population dynamics models used for stock assessment, although evolution of key life history traits may be of critical importance for population productivity, resilience to exploitation and to other anthropic pressures (Hard *et al.*, 2008). Specifically, despite a long-term interest (Gjerde, 1984 ; Hankin *et al.*, 1993) and recent advances (Barson *et al.*, 2015 ; Czorlich *et al.*, 2018), heritability in Atlantic salmon age at maturation is hardly ever accounted for in population dynamics model and especially in those used for stock-assessment (but see Bromaghin *et al.*, 2011 ; Piou *et al.*, 2015 ; Piou et Prévost, 2012). However, accounting for heritability is difficult to implement at the population scale and especially for natural population due to the lack of data and the complexity of life cycles. Our approach provides a way to detect heritability and predict response to selection for a trait within a population model embedded in a statistical framework for parameter estimation (by contrast with the simulation models proposed in Bromaghin *et al.*, (2011) and Piou *et al.*, (2015)), while also accounting for unexplained variability and sex-specific life-history. Quantitative genetics theory generally relies on strong assumptions, many of which are not met in the salmon case study. Discrepancies between the theoretical framework and the biological reality of our case study is a serious limitation to our approach. Among others, the theory behind both the offspring-parent regression and the Breeder's equation assume that there are no major gene with dominance and that there is no selection on correlated characters (Walsh et Lynch, 2018). These assumptions are either not respected (for instance *vgll3* has a sex-specific co-dominance; Barson *et al.* 2015 ; Czorlich *et al.* 2018) or likely not

respected. However, adapting the theoretical quantitative genetic framework to the specificity of the salmon life cycle for those assumptions would require substantial additional model development or additional data on allele frequency.

Still, we proposed some specific development that were needed to accommodate some specificities. Adapting quantitative genetic methods to population dynamic model required integrating additional random variability to the traits variations (Boëns, 2022 ; Heywood, 2005 ; Kelly et Williamson, 2000 ; Swain *et al.*, 2007 ; Walsh et Lynch, 2018 for adaptations of the Breeder's equation). The sex-specific life-history of salmon and the strong difference in maturation age between males and females (Mobley *et al.*, 2020 ; Siegel *et al.*, 2018 ; Tréhin *et al.*, 2021) required some specific adaptation of classical quantitative genetic methods that generally average trait over sexes (Walsh and Lynch, 2018) for this trait. Additionally, the use of the logit scale to model varations of maturation rate generated unusual problems that we solved by proposing an ad-hoc standardization of the mid-parent trait inspired by Bromaghin *et al.* (2011) (see appendix II). In summary, beyond the limitations of the approach, the models developed in this work proposed as a first step towards integration of heritability of age at maturation in a stock-assessment model applicable to stock assessment and management.

2. *Challenges and limitation in detecting heritability within a salmon population dynamic model*

Two different methods were applied to estimate heritability, the parent-offspring regression (Fox and Wolf, 2006) and the breeder's equation (Lush, 1937). Only the parent-offspring regression was successful in extracting a clear heritable signal. By constrast, integrating the Breeder's equation produced results highly dependent on the prior used.

The breeder's equation did not provide accurate estimates of heritability. As heritability of the trait was well-known (Barson *et al.*, 2015 ; Gjerde, 1984 ; Hankin *et al.*, 1993), the simulation model used to predict the response to selection was parameterized using estimates of heritability derived from an informative prior. .

The inability to detect selection within the Breeder's equation could be explained by the weakness of the selection in the historical observations. Alternatively, it could also indicate that the signal detected by the parent-offspring regression may be artifactual due to a confusion with the influence of growth during the first summer at sea. Indeed, when heritability was estimated with a parent-offspring regression, along with the integration of growth as a covariate to the probability of maturation, the heritable signal disappeared. The confusion between growth and

heritability may arise from the similar trends of the midparent trait and the growth anomalies (see appendix VII). Considering growth anomalies as a fully plastic response to the environment (as done here or in Tréhin et al. in prep) would then discredit our estimations of heritability. Alternatively, acknowledging that growth can also be in part heritable (Hutchings, 2011) could then explain the confusion between both signals without weakening our conclusion on heritability. A better description of the mechanisms linking maturation to the environment could help solving this dilemma. However, looking for those kind of proxies would require strong hypotheses on salmon migration route which knowledge are rather approximate and could vary over time (especially for 2SW, Dadswell *et al.*, 2010). The use of an integrative measure such as growth allow to avoid these hypotheses.

Our estimations of heritability are also dependent on several model assumptions, that influence estimations of the probability of maturation or the link between smolt cohorts and their parents. First our estimations of the probability of maturing as 1SW depend on assumptions made on the survival during the second year at sea (s_1 and s_2). Those parameters cannot be estimated from the data at hand and mostly derive from expertise (Chaput *et al*., 2003 ; Pardo *et al.*, 2021)). Those survival were fixed, with equal monthly mortality rate for 1SW and 2SW. This is however a strong hypothesis given the fact that 1SW and 2SW have different migration routes during the second year at sea and therefore do not share the same environment (Bradbury *et al.*, 2021 ; Dadswell *et al.*, 2010 ; Reddin *et al.*, 2012 ; Renkawitz *et al.*, 2015). Some literature support that one sea-winter salmons may have a survival rate twice as high as 2SW (Simmons *et al.*, 2021), for instance due to size-selective mortality. Mobilizing new data on salmons sampled at sea (Bradbury *et al.*, 2021 ; Gilbey *et al.*, 2021 ; Renkawitz *et al.*, 2015 ; Utne *et al.*, 2021a, 2021b) and developing modelling approaches to separate the survival before and after maturation decision is a key challenge for future research (Pardo *et al.*, 2021).

Second, the link between parent and offspring is highly dependent on the hypotheses made on spawners fecundity. For females, we used a new data on fecundity based on the link between fecundity and body length (Nevoux *et al.,* 2021), a significant improvement over previous models that used a fecundity constant over time (Olmos *et al.,* 2019 ; Tréhin et al., in prep ; ICES 2021). However the model assumes that there are no maternal effects , although it is known that the size of the female also has an effect on the energy content of eggs (Heinimaa et Heinimaa, 2004) and thus on the probability of survival during the juvenile phase. Less information exist to determine males fecundity and we assumed that 1SW and 2SW males had the same reproductive outputs. It is however likely that 2SW male may outperform 1SW, either

by a greater access to reproduction through behavioural selection (Mjølnerød *et al.*, 1998) or throughbetter spermatozoids motility and concentration (Gage *et al.*, 1995 ; Vladić and Järvi, 2001). However, our investigation highlighted that an increase in male 2SW fecundity generated only minor changes to the heritability estimations (Appendix XI).

Thirdly, we also simplified the salmon life cycle by excluding two reproductive strategies: Precocious salmon (also called sneaky males or mature parr male) and repeat-spawning salmon. Both strategies could significantly impact the link between parent and offspring which is critical to the detection of heritability. Precocious salmon can mature without experiencing sea migration. They are relatively poorly studied, at least in the Scorff river population, although their impact on population reproduction could be very important (Saura *et al.*, 2008). Indeed, their spermatozoids are more motile and concentrated, they have a higher gonadosomatic index (Gage *et al.*, 1995 ; Vladić and Järvi, 2001) and could fertilize more eggs than anadromous male, compensating their small size and subordination (Vladić et Järvi, 2001). Additionally such strategy may also be heritable and even correlated with the genetic structure for age at maturation (Aubin Horth et Dodson, 2004 ; DeFilippo *et al.*, 2019 for Pacific salmon), opening new perspectives on heritability studies including precocious males. Repeat spawners, which are able to reproduce several times during their life, experiencing another migration at sea between each reproduction, are also ignored. Their proportion vary among population, and could increase in less selective (suggesting less fishing activity) environment (Bordeleau *et al.*, 2019). We have little information about their fecundity but some studies documented that they have more eggs, but smaller and with lower survival rate, explained by the small amount of time spent at sea between reproductions (Reid et Chaput, 2012). Complementing the life cycle model by integrating precocious and repeat-spawning salmon proportion in the Scorff population is an avenue for future studies.

3. *Evolutionary equilibrium and short-term response to selection under fishing scenarios*

In addition to detecting heritability in age at maturation, we used our adaptation of the breeder's equation to predict its consequences by studying the response to the selection under several fishing scenario. Long-term simulations allowed us to derive evolutionary equilibrium, and short-term simulations allowed us to assess the potential speed of changes.

Simulations using the breeder's equation are generally considered reliable for a time frame of 15 generations (Fox and Wolf, 2006), so our long-term simulations should not be considered as

prediction: after tens of generations under selection it is highly likely that genetic variance and thus heritability would drop (Wolf and Lynch, 2018), consequently slowing or even preventing the attainment of the evolutionary equilibrium. Here long-term simulations were used only as a fast and empirical way to derive the equilibrium generated with the scenarios.

Equilibrium derived from the long-term simulations were quite sensitive to the harvest rate scenarios. Indeed, four scenarios with harvest rate for 1SW and 2SW ranging between 6 and 16% had equilibrium ranging from 15 to 90% 1SW. Prediction of the evolutionary equilibrium but also concerning the short-term response to selection are likely strongly dependent to the assumptions on the selection differential, such as mortality at sea and fecundity. Interestingly, the equilibrium derived from the status-quo scenario (mean harvest rates observed over the time-series) is quite far from the range of observed values. This suggests the system could be relatively far from its equilibrium and proportion of 1SW should increase in order to reach the equilibrium - given that the genetic potential for such evolution exists. However, this could also indicate that the selection differential that we introduced favors 1SW more than in reality, for instance due to error in mortality rates or fecundity.

Predicted response to selection were dominated by the unexplained random variations. Although very large uncertainties are generated by unexplained random variations, trends towards the evolutionary equilibrium are still noticeable within 15 generations.

4. Perspectives

Our results provide valuable insights for management. They show that, currently, fishing intensity is mainly focused on 2SW salmon, likely impacting their proportion in the future. In parallel, environmental changes would also be in disfavor of 2SW salmon (Piou *et al.*, 2015), potentially accelerating their collapse. Management strategies avoiding targeting two-sea winter fish may need to be considered in order to ensure the population resilience (Piou *et al.*, 2015).

Here, we developed a model, fitted to the available data from the survey of the Scorff population, one of the ICES index rivers (ICES, 2021). But the structure of our model is transferable to other situations such as index rivers that serve as a reference for regional or national management or even for models built at a larger scale, like the one developed to assess A. salmon stock status at the scale of the North Atlantic basin (Olmos *et al.*, 2019, 2020 ; ICES 2021). Such transfer would likely help generalizing our results and provide new insight to the demographic and ecological mechanism over a large number of populations.

The marine phase remains a black box in the salmon life history. Migration at sea remained poorly understood (Bradbury *et al.*, 2021), while also being prone to changes (Morita, 2019). Improving our understanding of this phase is needed to provide reliable model, especially when considering the potential for natural selection in a changing world. Adams *et al.* (2022) suggested that Atlantic salmon migration cost may increase and become maladaptive because of shifting environmental conditions. They provided evidence that in future, salmon and especially males could forego migration at sea and become freshwater. Future studies considering numerous salmon trait, their heritability, and their evolution through environmental change and fisheries would be necessary to have a better overview and prediction of salmon stock evolution to adapt the best management measures.

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Appendix I - Effect of smolt age on maturation rate

During model development, we considered including an effect of smolt age on maturation rate. Two different hypotheses are found in the literature. Hankin *et al.* (1993), suggest that younger smolts are more likely to mature during the first year at sea considering as fast growth in river may translate into fast growth at sea as well. On the other hand, Mobley *et al.* (2020), propose that younger smolts that spent little time in river would require more time at sea to grow and reach a threshold size. Consequently, a smolt 1 would be more likely to mature after two years at sea. We decided to test these hypotheses using our model by implementing the smolt age in the maturation rate:

$$logit(p\_maturation_{t,sex,age}) = \mu + \alpha_{sex} + \beta_{age} + \varepsilon_{t,sex} \qquad (A1)$$

$$with \ \mu \sim N(0, 0.25), \alpha_{sex} \sim N(0, 0.25), \beta_{age} \sim N(0, 0.25)$$

$$and \ \varepsilon_{t,sex} \sim N(0, \sigma_{mat,sex}^2)$$

This model assumes random variations among years in maturation rates around a grand mean (denoted μ) common between sex and age, a sex-specific term (α_{sex}) to account for differences in mean maturation rate between sexes but also an age of smolt specific term (β_{age}) to account for the possible difference in mean maturation rate between smolts of different age. Additionally, a sex-specific random component $\varepsilon_{t,sex}$ represent the effect of the environmental variability.

The results of this work are in favor of the first hypothesis suggesting that smolt 1 are more likely to mature during the first year at sea (Figure A1). Large uncertainties and the limited amount of data on smolts 2 however limit the strength of this result, which would certainly be of interest for future study.
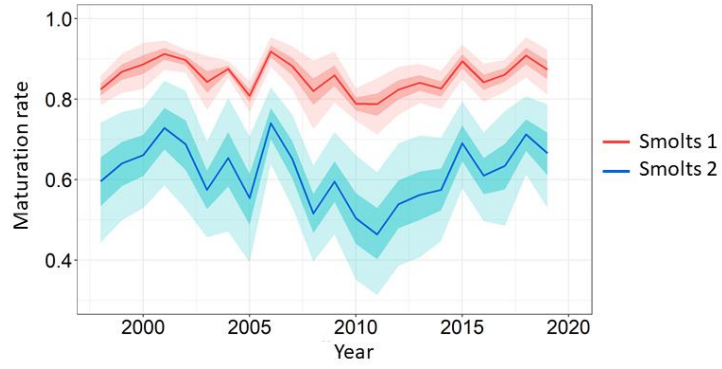
Figure A1: Temporal fluctuations for the maturation rate for smolt 1 and smolt 2. Solid lines with shaded areas represent the median, the 50% and the 90% credibility interval of the posterior distribution of the maturation rate.

Appendix II – Calculation of the midparent trait

The midparent trait (or midparent value) is defined as the average of the trait value (here the maturation rate) of the parents (father and mother). This value is frequently used to study quantitative traits in heritability studies (Walsh and Lynch, 2018). In our study we used two different midparent trait: before and after selection.

a. Before selection

The midparent trait before selection is calculated from the proportion of 1SW males ($1SW\ before\ \male_t$) and females ($1SW\ before\ \female_t$) salmons after the maturation decision and thus before the survival in sea (s_1 and s_2) and the catches in river (*h1SW and h2SW*).

$$logit(Midparent\ before_t) = \frac{logit(1SW\ before\ \female_t) + logit(1SW\ before\ \male_t)}{2} \quad \text{(A2)}$$

With

$$1SW\ before\ \female_t = \frac{Nmature\ \female_t}{Nmature\ \female_t + Nnonmature\ \female_t} \quad \text{(A3)}$$

And

$$1SW\ before\ \male_t = \frac{Nmature\ \male_t}{Nmature\ \male_t + Nnonmature\ \male_t} \quad \text{(A4)}$$

Where $Nmature\ \female_t$ and $Nnonmature\ \female_t$ ($Nmature\ \male_t$ and $Nnonmature\ \male_t$) are the abundances of females (and males) maturing and non-maturing at the end of the first summer at sea.

b. After selection

The midparent trait after selection is calculated from the proportion of 1SW males ($1SW\ after\ \male$) and females ($1SW\ after\ \female$) salmon at year *t* just before the reproduction and thus after the survival in sea (s_1 and s_2) and the catches in river (h1SW and h2SW)

$$logit(Midparent\ after_t) = \frac{logit(1SW\ after\ \female_t) + logit(1SW\ after\ \male_t)}{2} \quad \text{(A5)}$$

With

$$1SW\ after\ ♀_t = \frac{N1SWspawners\ ♀_t}{N1SWspawners\ ♀_t + N2SWspawners\ ♀_t} \tag{A6}$$

And

$$1SW\ after\ ♂_t = \frac{N1SWspawners\ ♂_t}{N1SWspawners\ ♂_t + N2SWspawners\ ♂_t} \tag{A7}$$

Where $N1SWspawners\ ♀_t$ and $N2SWspawners\ ♀_t$ ($N1SWspawners\ ♂_t$ and $N2SWspawners\ ♂_t$ are the abundances of females (and males) 1SW and 2SW at year *t* that are able to reproduce.

c. *Standardization of the midparent trait*

One of the particularities of the trait used in this study is that the values are different between males and females. We have therefore a level effect on the midparent trait. Additionally traits are calculated in logit scales, with a distortion for values close to one in the natural scales. For instance, the probability of maturing has a much larger variance for males compared to females in the logit scale, despite having similar variances in natural scale. Using equations A2 and A5 would then have several issues : (1) midparent trait would be dominated by the variation in male trait, due to the larger variance and (2) the difference in trait for males and females offsprings would not be accounted for. To avoid such caveat, we propose a sex-specific standardization of the midparent trait, inspired from Bromaghin *et al*. (2011). The mean and variance of father and mother trait are standardized to the mean and variance of male or female trait, using equations A8 and A9:

$$Midparent\ ♀_t = \frac{1SW\ ♀_t + \frac{1SW\ ♂_t - μ♂}{σ♂} * σ♀ - μ♀}{2} \tag{A8}$$

$$Midparent\ ♂_t = \frac{1SW\ ♂_t + \frac{1SW\ ♀_t - μ♀}{σ♀} * σ♂ - μ♂}{2} \tag{A9}$$

Where $1SW\,\male_t$ and $1SW\,\female_t$ are the proportions of 1SW males and females at year t, μ and σ are the sex-specific mean and standard deviation of 1SW salmons in the population during the time-series. Such standardization is then applied both for midparent trait before and after selection, both when using the offspring-parent regression and the breeder's equation.

Appendix III – Calculation of the mean exploitation rates

The exploitation rates for 1SW and 2SW salmons are needed to build scenarios for long term simulations. We decided to build the first scenarios based on the mean exploitation rate estimated with the model (Figure A3).
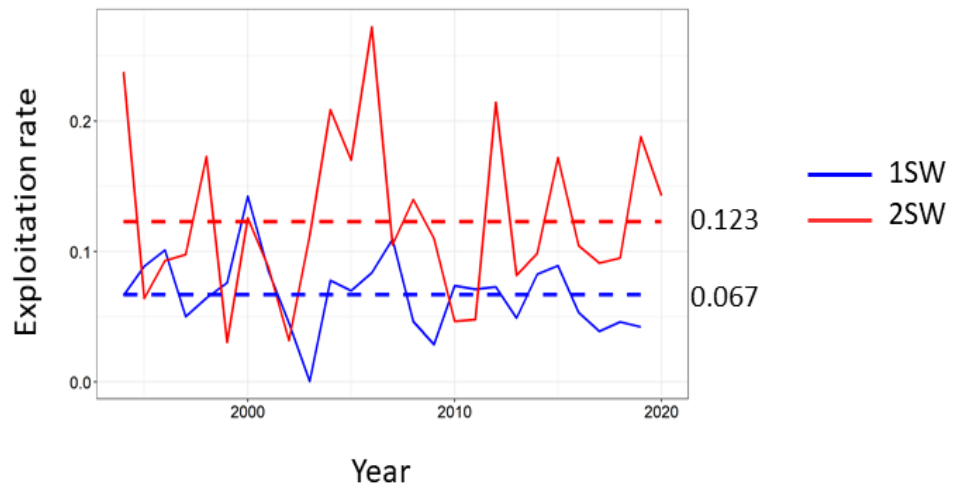
Figure A3: Exploitation rate estimated in the model for 1SW and 2SW (solid lines). Mean exploitation rates (dotted lines) have been calculated for all years.

Appendix IV – Priors used in the model

In total, 19 priors have been used in this model. Among them 18 are weakly informative and 1 is informative (Heritability component of maturation probability using the breeder's equation). This prior has been chosen in order to have a distribution between 0 and 1 centered on 0.2. For Normal and log-normal distribution, the first terms in bracket is the mean, and the second is the precision which is the reciprocal of the variance (precision $= 1/\sigma^2$)

Table A1: Prior distributions used for the model parameters.

Parameter	Name	Prior distribution
Carrying capacity	k	Log-normal (10.7, 1)
Maximum survival	α	Beta (0.14, 1.86)
Proportion of smolt 1	p_smolt_cohort	Beta (2, 2)
Total smolt abundance (log scale)	Nsmolt	Log-normal (0, 0.01)
Total 1SW return abundance (log scale)	N1SW	Log-normal (6.5, 1)
Total 2SW return abundance (log scale)	N2SW	Log-normal (4.5, 1)
Mean for proportion of females in smolts	Prop3f	Beta (10, 10)
Mean for proportion of females in 1SW	Prop6f	Uniform (0, 1)
Mean for proportion of females in 2SW	Prop9f	Uniform (0, 1)
Exploitation rates (1SW and 2SW)	h1SW and h2SW	Beta (1, 2)
Mean survival probability	ν	Normal (0, 0.1)
Standard deviation for common component of temporal variability in survival probability	γ	Uniform (0, 5)
Common component of maturation probability	μ	Normal (0, 0.25)
Sex-specific component of maturation probability	α_{sex}	Normal (0, 0.25)
Heritability component of maturation probability (offspring-parent regression)	h^2	Uniform (0, 1)
Heritability component of maturation probability (breeder's equation)	h^2	Beta (3, 9)
Slope of the relationship between the growth covariates and the maturation probability	β_{sex}	Normal (0, 0.25)
Standard deviation for sex-specific component of temporal variability in maturation probability	$\sigma^2\varepsilon_{sex}$	Uniform (0, 5)

Appendix V – Convergence analysis

The convergence of MCMC chains has been assessed through a Gelman-Rubin test and the observation of the effective sample size for each model used in this study (we decided to show two of them in this section). The Rhat compare the intra-chain variance to the inter-chain variance and the effective sample size determine the size of the sample that has the same amount of probabilistic information compare to a random sample.

For both models used, all Rhat statistic are inferior to 1.05 (Figures A4 and A6) and all the effective sample size are superior to 1000 (Figures A5 and A7).

a. Model using offspring-parent regression and an environmental proxy
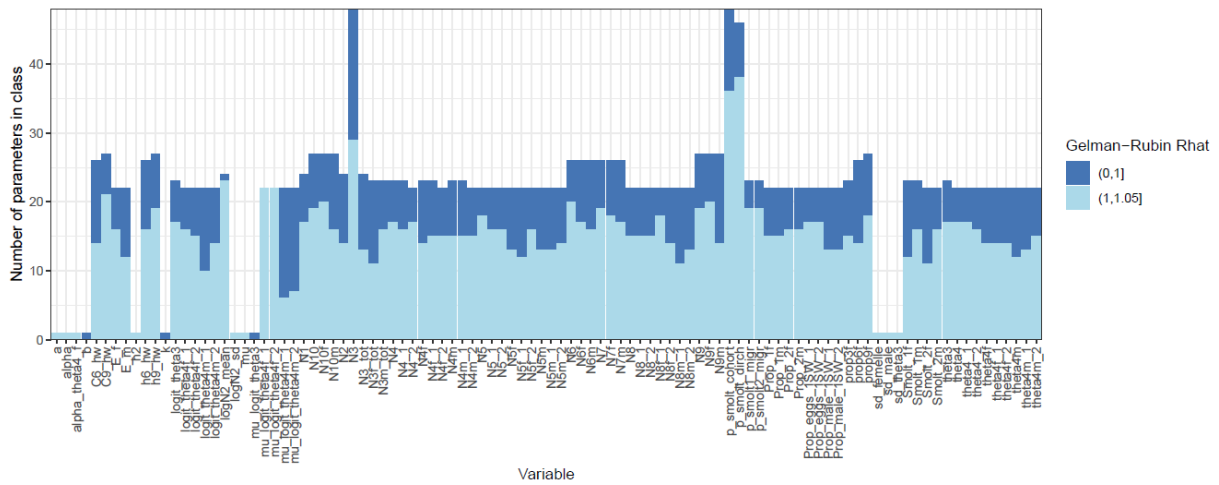
Figure A4: Rhat statistic for all parameters and variables used in the model.
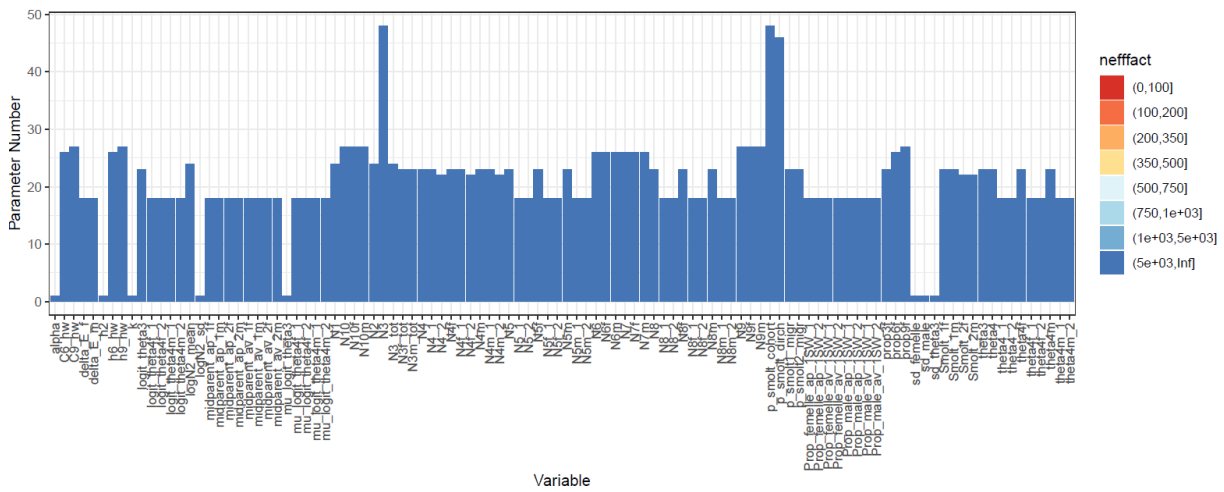
Figure A5: Effective sample size for all parameters and variables used in the model
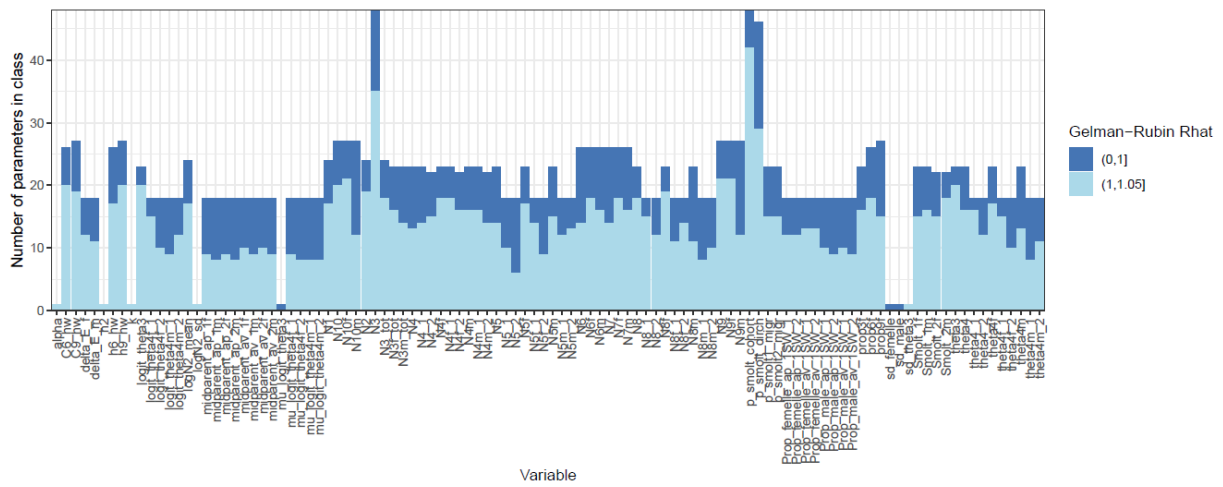
Figure A6: Rhat statistic for all parameters and variables used in the model.
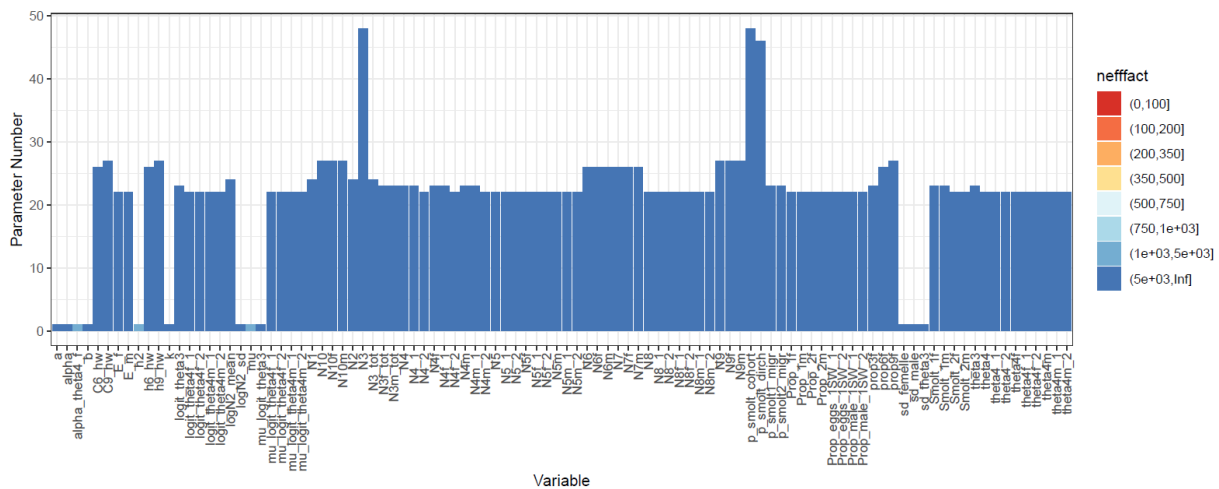

Figure A7: Effective sample size for all parameters and variables used in the model.

Appendix VI – Fit assessment analysis

The two models used in this study exhibits a good fit to the different data sources (Figures A8 and A9).

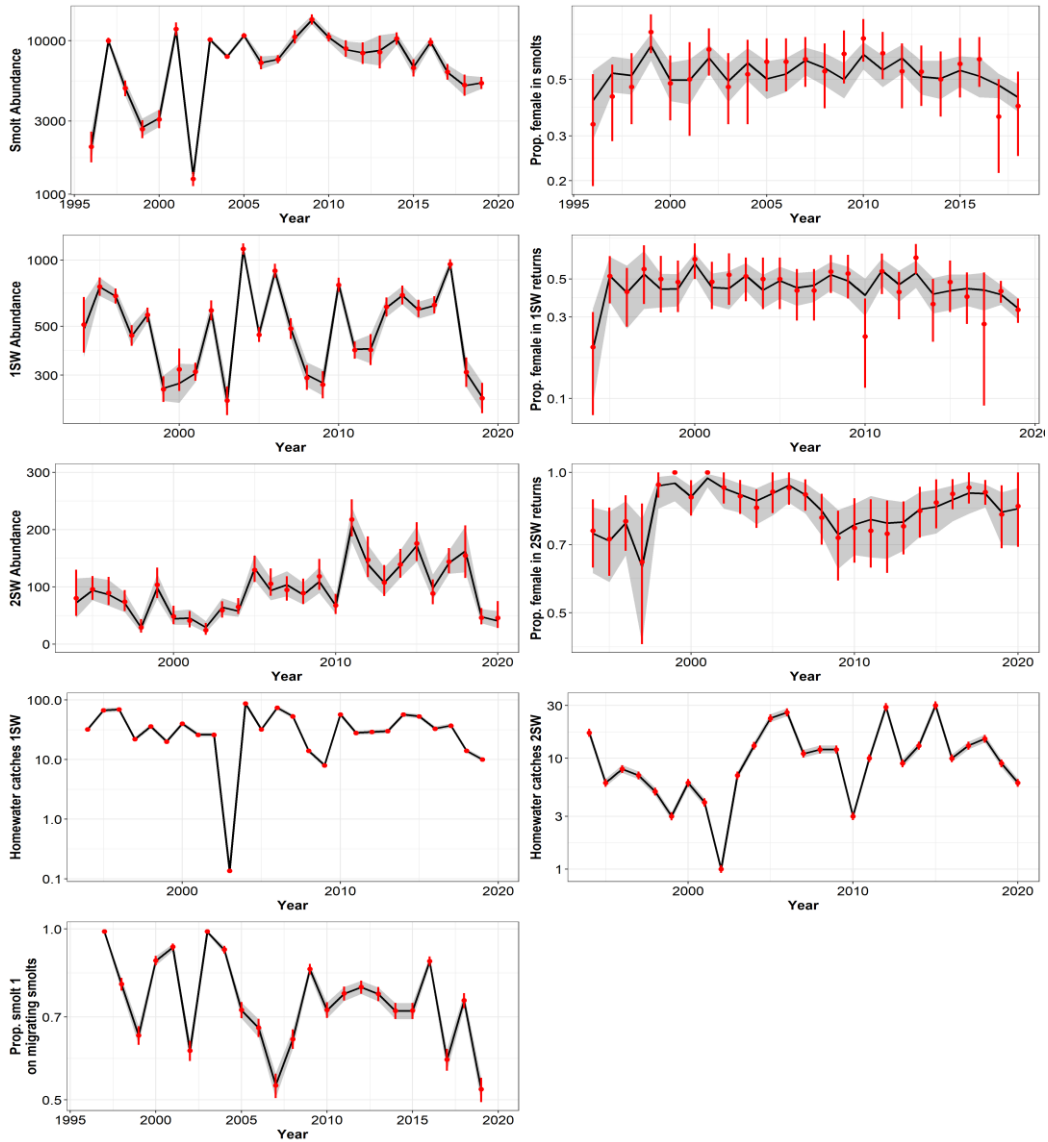a. *Model with offspring-parent regression and environmental proxy*

Figure A8: Fit to abundance, sex ratio, and smolt age data including temporal variability on both survival and maturation and inter-annual variation in the maturation between males and females. Black solid lines with shaded areas represent the median and the 95% credibility interval of the marginal posterior distribution of abundance, sex ratio, and smolt age proportion. Red dots with error bars represent the median and 95% credible interval of the observation distribution used in the integrated model.
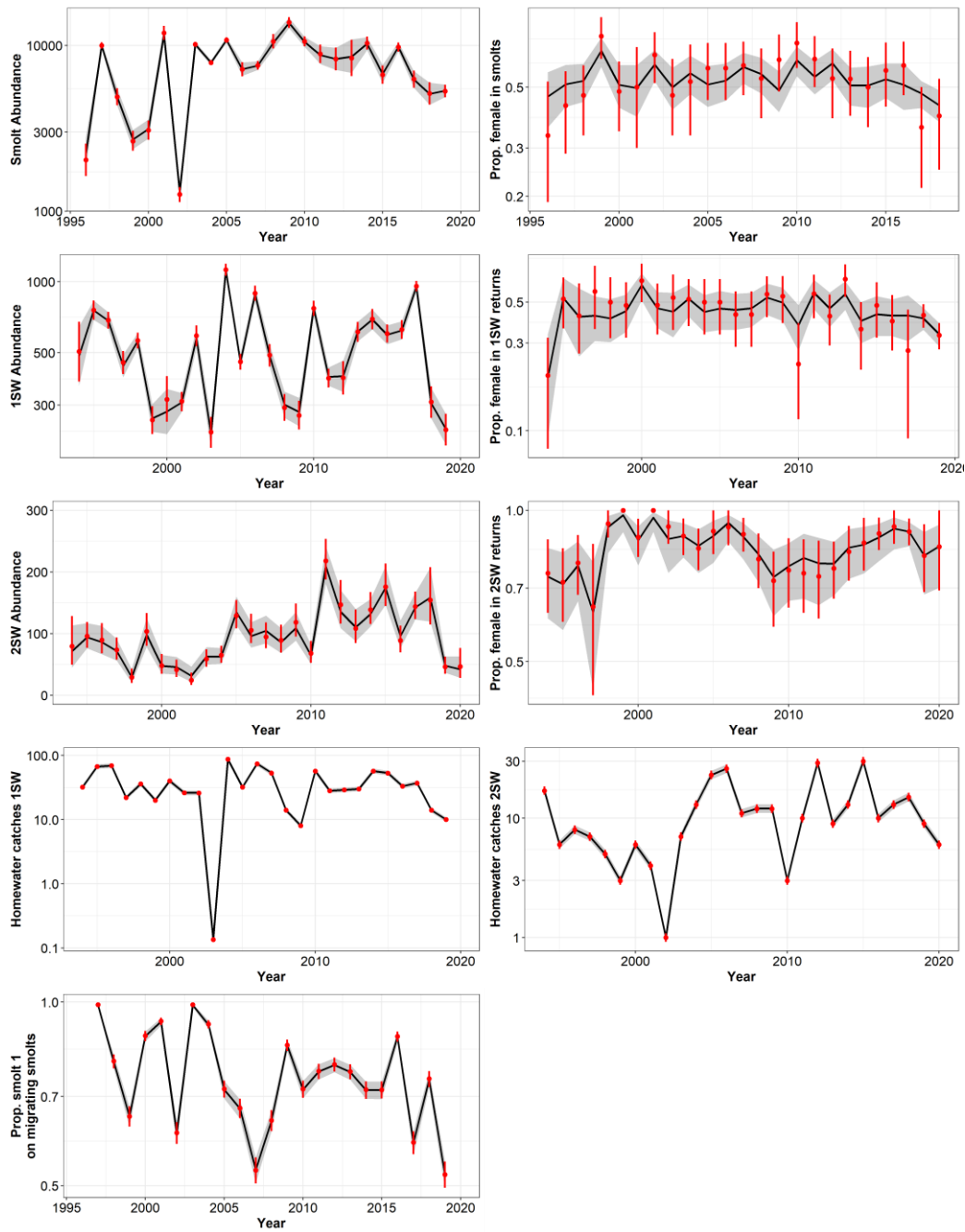
b. Model with breeder's equation

Figure A9: Fit to abundance, sex ratio, and smolt age data including temporal variability on both survival and maturation and inter-annual variation in the maturation between males and females. Black solid lines with shaded areas represent the median and the 95% credibility interval of the marginal posterior distribution of abundance, sex ratio, and smolt age proportion. Red dots with error bars represent the median and 95% credible interval of the observation distribution used in the integrated model.

Appendix VII – Synchrony between growth anomalies and proportion of 1SW

Variations of the midparent traits and growth anomalies can be compared with a first section from 1997 to 2007 showing high values for both variables (Figure A10). Then a sharp decline in 2008 and a low-value plateau are observed for both variables. This correlation between the midparent trait and the growth anomaly could explain the confusion of these two variables in the model and the loss of the heritable signal.
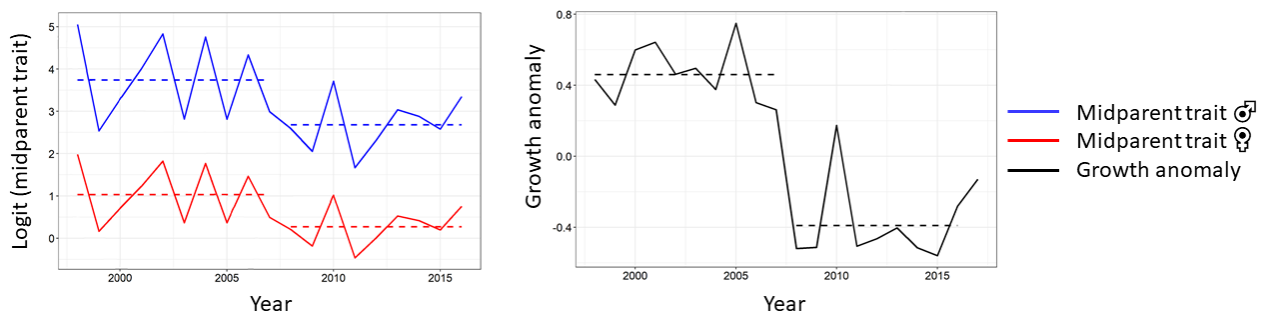

Figure A10: Temporal fluctuations for the midparent trait (left) and the growth anomaly (right). Dotted lines represent the mean of each variable on a certain lap of time.

Appendix VIII – Confidence interval of long-term simulation

Scenarios 1, 2, 3 and 7 have a maturation rate confidence interval increase very quickly and reach the minimum and the maximum possible values (0 and 1) in the 1000 years of simulation. For the other scenarios the confidence interval decreases as a function of the exploitation rate provided leading to scenarios 6 and 8 to have relatively small confidence interval at the end of the simulation.
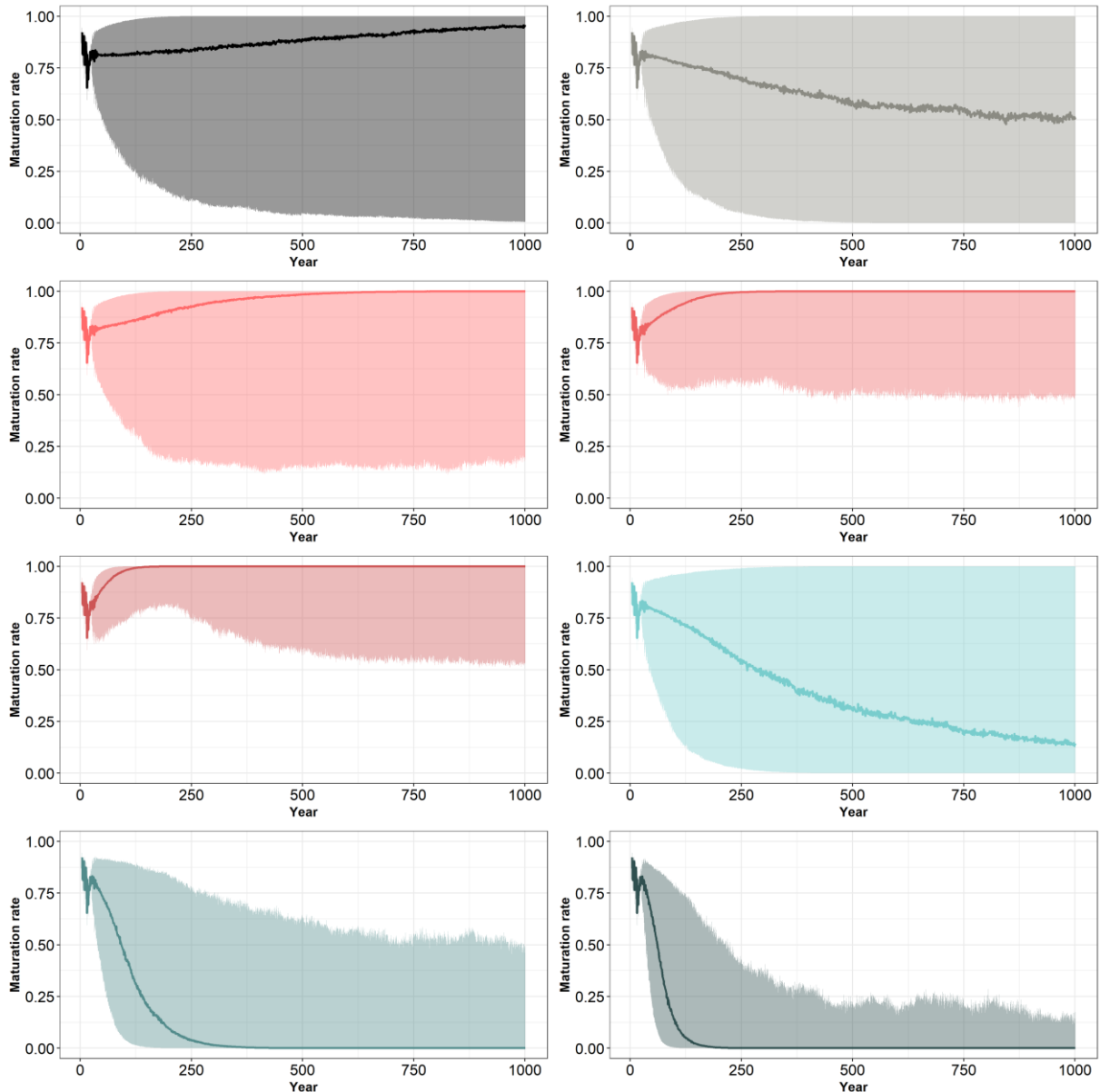

Figure A11: Temporal fluctuation for the hindcasted and forecasted maturation rate for each scenario (1 at the top left and 8 at the bottom left). Solid line with shaded area represents the median and the 90% credibility interval of the posterior distribution of the maturation rate.

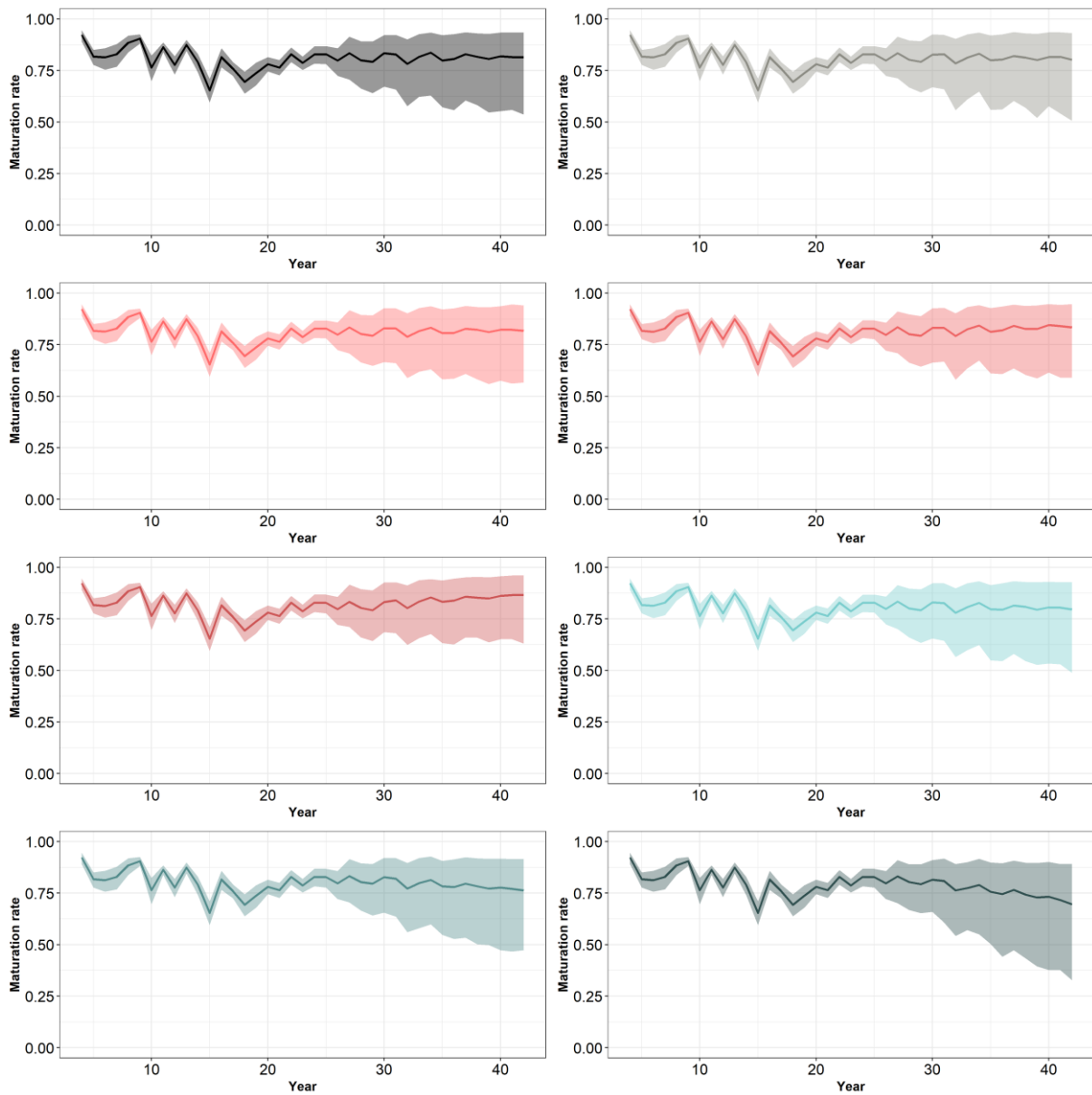# Appendix IX – Confidence interval of short-term response to selection

Figure A12: Temporal fluctuation for the hindcasted and forecasted maturation rate for each scenario (1 at the top left and 8 at the bottom left). Solid line with shaded area represents the median and the 90% credibility interval of the posterior distribution of the maturation rate.

Appendix X – 1SW and 2SW abundance following simulations

To ensure that no scenarios would drive the salmon populations extinct, we monitored population size for both 1SW and 2SW. Results follows our expectation: there are no situations where both 1SW and 2SW go extinct and 1SW or 2SW population size only go to 0 in situations where they are strongly selected against.
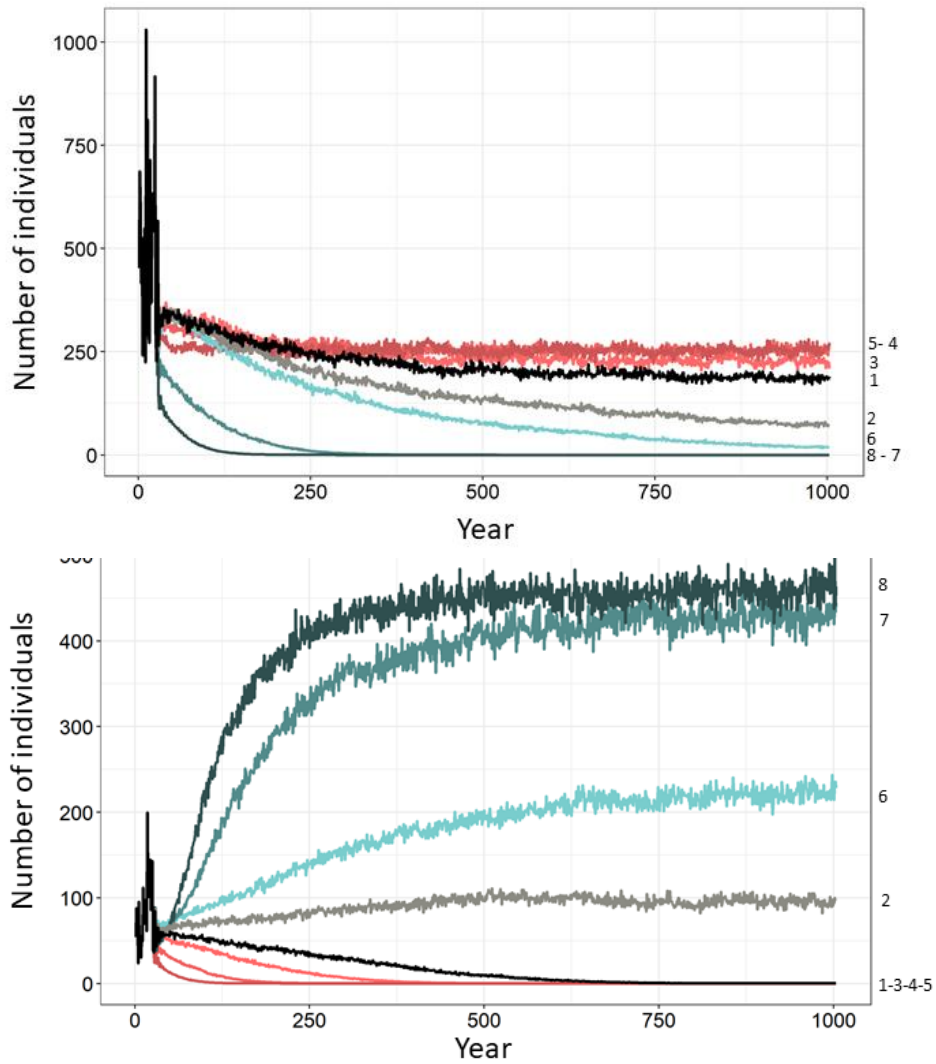

Figure A13: Comparison of the abundances of 1SW (top) and 2SW (bottom) on 1000 years based on the different scenarios of exploitation rate.

Appendix XI – Sensitivity to the hypothesis of male fecundity

To test the robustness of our heritability estimate against the assumption of equal male fecundity for both 1SW and 2SW, we tested a situation where 2SW males where 50% more fecund than 1SW males. Without doubt, posterior distributions are highly similar and our estimations are quite robust to this assumption.
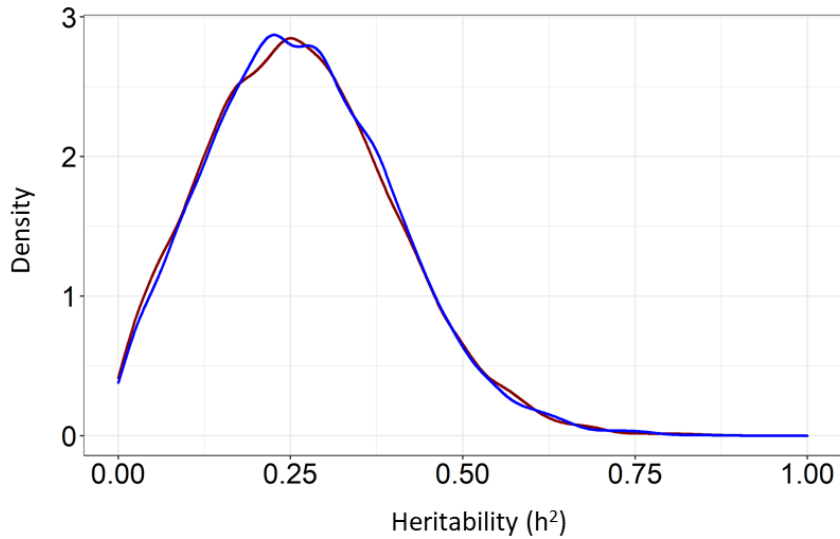

Figure A14: Posterior distribution of the heritability parameter from offspring-parent regression with similar fecundity between 1SW and 2SW (blue) and with a 50% increase of 2SW fecundity (red).

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Titre français : Quantifier les composantes héritables et plastiques de l'âge à maturation chez le saumon atlantique et prédire la réponse à la sélection par les pêcheries.

Titre anglais : Quantifying heritable and plastic components of age at maturation in Atlantic salmon and predicting response to selection by fisheries.

Résumé : Les populations sauvages de saumon atlantique (*Salmo salar*) ont connu un déclin de leur abondance dans les dernières décennies, accompagné par des changements dans des traits phénotypiques importants comme le temps de séjour en mer. Ce temps passé en mer est connu pour être fortement héritable mais aussi sous influence de l'environnement. Séparer ces deux composantes devient alors essentiel pour quantifier l'influence de multiples facteurs de pression comme les changements dans l'écosystème marin ou la pêche. Nous proposons un modèle Bayésien à espace d'états permettant de séparer les composantes plastiques et héritables de la variabilité temporelle de l'âge à maturation d'une population de saumons du Scorff. En adaptant une régression parent-enfant, nous pouvons estimer l'héritabilité de la probabilité de maturation après un an en mer à l'aide d'un modèle basé sur des données populationnelles. La réponse plastique, que l'on peut donc distinguer de la composante héritable, explique une plus forte partie de la variabilité du trait. En intégrant l'équation du sélectionneur dans le modèle, nous pouvons à la fois déterminer l'équilibre évolutif et prédire la réponse à court terme à la sélection selon différent scénarios de pêche. Dans un contexte où la pêche et/ou l'environnement rencontré pendant la migration marine peuvent engendrer de la mortalité différentielle entre les âges de mer, ces résultats constituent un premier pas pour en prédire les conséquences en termes de dynamique des populations et d'évolution des traits de vie au niveau populationnel.

Abstract : Wild populations of Atlantic salmon (*Salmo salar*) have experienced a decline in abundance in recent decades, accompanied by changes in important phenotypic traits such as time spent at sea. Time spent at sea before reproduction is known to be highly heritable but also environmentally influenced. Separating the plastic and heritable component in this evolution becomes essential to quantify the influence of multiple pressure factors such as changes in the marine ecosystem or fishing. We propose a Bayesian state-space model to separate the plastic and heritable components of the temporal variability of the age at maturation of a salmon population in the Scorff River. By adapting a parent-offspring regression we can successfully estimate the heritability of the probability of maturation after one year at sea using a model based on population data. The plastic response, which can thus be distinguished from the heritable component, then explains only part of the variability of the trait. By integrating the breeder's equation into the model, we can both derive empirically evolutionary equilibrium and predict short-term response to the selection under several fisheries scenarios. In a context where fishing and/or the environment encountered during marine migration can generate differential mortality between the ages of the sea, these results constitute a first step to predict the consequences in terms of population dynamics and evolution of life traits at the population level.

Mots-clés : *Salmo salar*, dynamique des populations, héritabilité, plasticité, maturation, modélisation, Bayésien

Key Words: *Salmo salar*, population dynamics, heritability, plasticity, maturation, modelling, Bayésian