Changes in sex ratio and fecundity of salmonids

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Abstract

In salmonids, life history traits (e.g. growth, age or size at maturation) differ strongly between sexes. They are also susceptible to vary between populations and/or over time as a response to changes in the marine environment. However, those variations between sex, populations and time are difficult to observe from empirical monitoring. Consequently, population dynamic models used to set conservation limits and fishing quotas (known as Stock Assessment Models or SAMs) most often assume that vital rates do not differ between males and females, and/or consider fixed values of sex ratio and fecundity. These strong assumptions could lead to inappropriate management decisions based on biased population productivity estimates.

Thanks to new data and methods developed in the SAMARCH project, we assessed the long-term trends in the sex ratio at different salmonid life stages (smolts and adults) in the SAMARCH rivers. Individual measurements of length and fecundity available on a large sample of females were also collated. Statistical models were developed to characterize changes in sex ratios and female fecundity and to investigate the factors contributing to these changes (e.g. body size, age). Results highlight that the sex ratio of returning fish was relatively stable for each sea age class over time, but that the average fecundity declined by 15% between 1985 and 2018, mostly driven by a decline in the mean body length and weight of returning multi sea-winter females. This suggests that SAMs might systematically overestimate egg deposition, particularly in recent years, which could lead to overstate compliance with conservation limits. The novel data on sex ratio and fecundity will be incorporated in new SAMs to reduce their possible bias. This will encourage managers to derive more realistic conservation limits that recognize the changing ratio of females and the changes in mean body size within each sea age class.

Introduction

The fecundity of salmonids, defined as the number of eggs produced by females in the population, is a key parameter in population dynamics models and stock status. Typically, fecundity is used to calculate the total egg production potentially spawned by a population in a particular year, by multiplying the number of mature females (or mature individuals multiplied by the proportion of females) by the average fecundity. This is a key input to estimate the "stock" in classical stock-recruitment analysis that are one of the main rationale to estimate biological and management reference points, such as optimum spawning escapement or conservation limits (Prévost and Chaput 2001, Rivot et al. 2001, Hilborn and Walters 2013).

In salmonids, spatial and temporal variations in sex ratio and fecundity are often overlooked due to the difficulties collecting field data on traits that are not directly observable. As a consequence, population dynamic models that form the basis of stock assessment tools used to set management reference points, conservation limits and fishing quotas, most often assume fixed values of sex ratio and fecundity that are expected to vary over time. For instance, White et al. (2016) developed a model to estimate conservation limits on Irish rivers by using river-specific life history traits, but the models do not consider different parameters between males and females and consider fixed values with no temporal variations. Stock assessment models developed by the Working Group on the North Atlantic Salmon of the International Council for the Exploration of the Sea (ICES/CIEM WGNAS) consider the dynamic of large stock units aggregated at the scale of countries or regions with constant parameters between males and females and over time (Chaput 2012, Olmos et al. 2019).

However, accumulated evidence suggests that those life history traits may be highly variable between populations and have changed over time, and particularly in response to recent environmental changes. Accounting for spatial and temporal variations in the sex ratio and in the fecundity of salmonids populations will strengthen population dynamics models by reducing their possible biases. This will encourage managers to derive more realistic conservation limits that recognize the changing ratio and fecundity of females within each sea age class.

Thanks to new data and methods developed in the SAMARCH project, we assessed the long-term trends in sex ratios of different salmonids life stages (smolts and adults) in the SAMARCH rivers. Individual measurements of length and fecundity available for a large sample of females were also collated. Statistical models were developed to characterize changes in sex ratios and female fecundity and to investigate factor contributing to these changes (e.g., body size, age). These novel data on sex ratio and fecundity will be incorporated as improvements to stock assessment models, as part of SAMARCH task WP-T3.4.

1. Changes in sex-ratio of salmonids

Study populations and sample size

Changes in sex ratio of Atlantic salmon (*Salmo salar*) were investigated on five SAMARCH rivers over the last 40 years (Figure 1). For each river and year, 30 individuals from the following 3 life stages were sampled: smolts, adults returning after 1 winter at sea (1SW) and adults returning after 2 winters at sea (2SW) (Table 1).

Figure 1. The five rivers of the SAMARCH project.

River	Atlantic salmon			
	smolt	years	**adult**	**years**
Scorff	582	1995-2018	1612	1987-2018
Sélune	768	1985-2017	1816	1987-2017
Bresle	202	2008-2018	641	1985-2018
Frome	*	2006-2018	*	1971-2018
Tamar	*	2002-2017	821	1986-2018

Table 1. Number of individuals sexed as part of the SAMARCH project by life history stage and river. Analyses are still ongoing for some rivers and life history stage (*).

Molecular sexing

The sex of a sample of salmonids was assessed using molecular tools. Genomic DNA was extracted from a scale of each selected individual. A q-PCR multiplexing based on fluorescence (SYBR Green)(Morrison et al. 1998) was then performed to identify the sex

of each fish using two primers specific to salmonids. One as a reference gene (Fab3, targeting a fatty acid gene) amplified for both sexes as a control and a specific primer for sexing, specific to the Y chromosome (Yano et al. 2013), amplified for males only.

Data analysis

We analyzed the temporal variation in sex ratio of smolts and adults using general additive models GAMs (Wood 2017) to account for the potential non-linearity of the response over time. Statistical analyses were run with R (R-3.5.1), using the gam() function as implemented in the R-package mgcv, 1.8-31 (Wood 2017). GAMs were built assuming a Binomial sampling distribution and a logit link function, and a smoothed function of time. Because the time series from each river differ in length, independent models were built for smolts and adults for each river. An additional effect of age (2 smolt ages, and 2 adult ages, respectively) was tested as a fixed effect or in interaction with the smooth time trend. Starting with the most complex model (including a fixed effect of age and an interaction between the age and the time trend), nested models were compared using Akaike information criterion (AIC) (Burnham and Anderson 2002) in a stepwise approach.

Temporal trends in the sex-ratio of smolts

The sex ratios (calculated here as the proportion of males) of salmon smolts sampled in the Bresle (mean = 0.23, sd = 0.15), Sélune (mean = 0.35, sd = 0.11) and Scorff (mean = 0.47, sd = 0.11) rivers are always biased towards females, with a very strong bias towards females for the Bresle river. There is no effect of the smolt age on the sex-ratio. Smolt sex ratio is constant over the study period in the Sélune and Bresle, whereas the proportion of males observed in the Scorff decrease from 1995-2010 before returning to its former level by 2018 (Figure 2).

Figure 2. Change in the sex-ratio of salmon smolts over time in the SAMARCH rivers: a) Bresle, b) Sélune, c) Scorff. Symbols represent mean annual sex ratio in age 1 (○) and age 2 (△) smolts. Lines represent the best fitted GAM model.
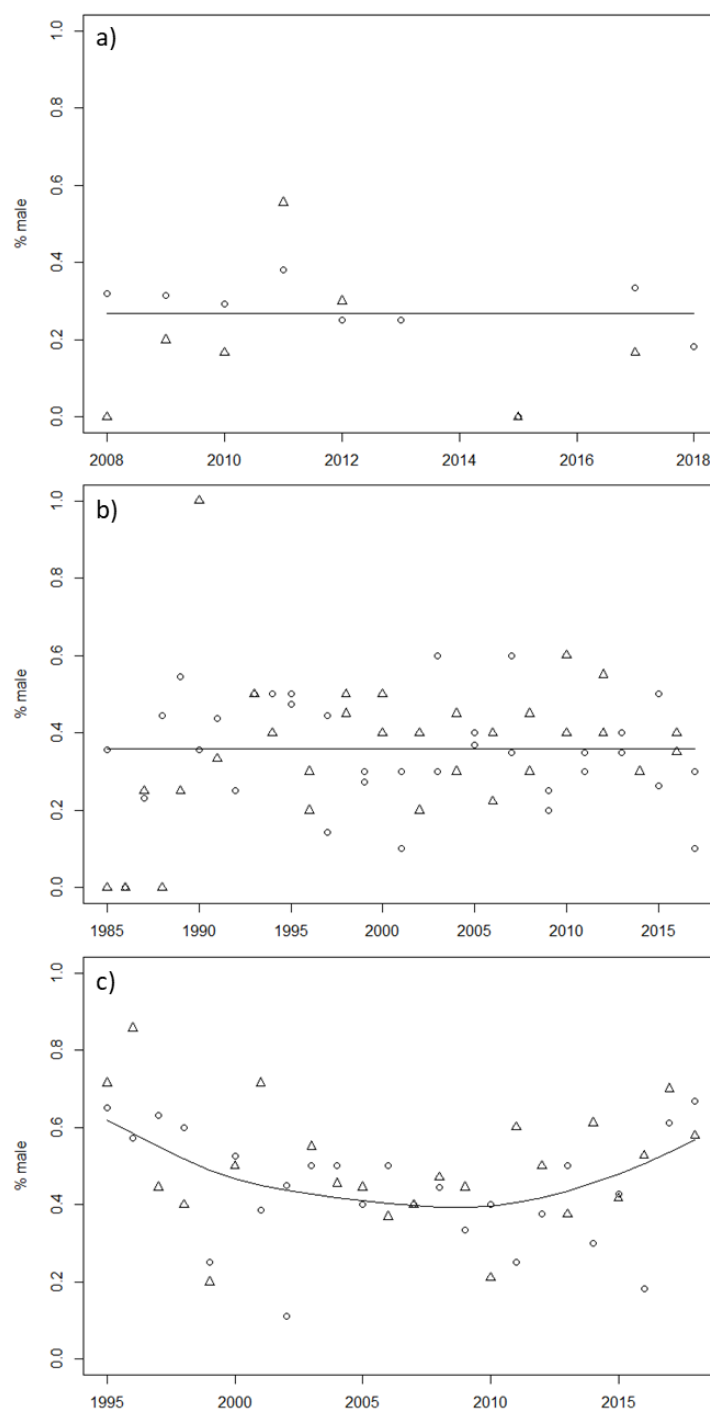

Temporal trends in the sex-ratio of returning adults

The sex ratios of adults show a very similar pattern on all SAMARCH rivers, e.g. Bresle, Sélune, Scorff and Tamar rivers (Figure 3). The sex-ratio of salmon returning after 1 winter at sea is close to parity (i.e., 1:1), whereas it is highly biased towards females in salmons

returning after 2 winters at sea (Figure 3). Interestingly, the sex ratios measured in returning adults differ from the sex-ratios measured among out-migrating smolt. In particular, the initial bias towards females detected in smolts from the Bresle is not observed any longer in 1SW returning fish, thus indicating sex-specific demographic mechanisms taking place during the marine phase.

Some temporal variability in age-specific sex-ratio is detected on the Bresle and Scorff, whereas sex-ratio is rather constant on the Sélune and Tamar over the study period. The values of sex-ratios used in ICES Pre Fishery Abundance stock assessment models (Chaput 2012, ICES 2020) (dashed lines in Figure 3) fit well to the sex-ratio observed in the Sélune (1SW), Scorff (1SW and 2SW) and Tamar (1SW), but overestimate the proportion of males in the Bresle (1SW and 2SW), Sélune (2SW) and Tamar (2SW), thus highlighting the need to consider between populations variations on sex ratios in stock assessment models instead of average values.

Figure 3. Change in the sex-ratio of salmon adults over time in the SAMARCH rivers: a) Bresle, b) Sélune, c) Scorff and d) Tamar. Symbols represent mean annual sex ratio in 1SW (black) and 2SW (red) returning adults. Solid lines represent the best fitted GAM model. Dotted lines represent values of sex-ratio used in PFA stock assessment models used by ICES for France or England & Wales (ICES 2020).
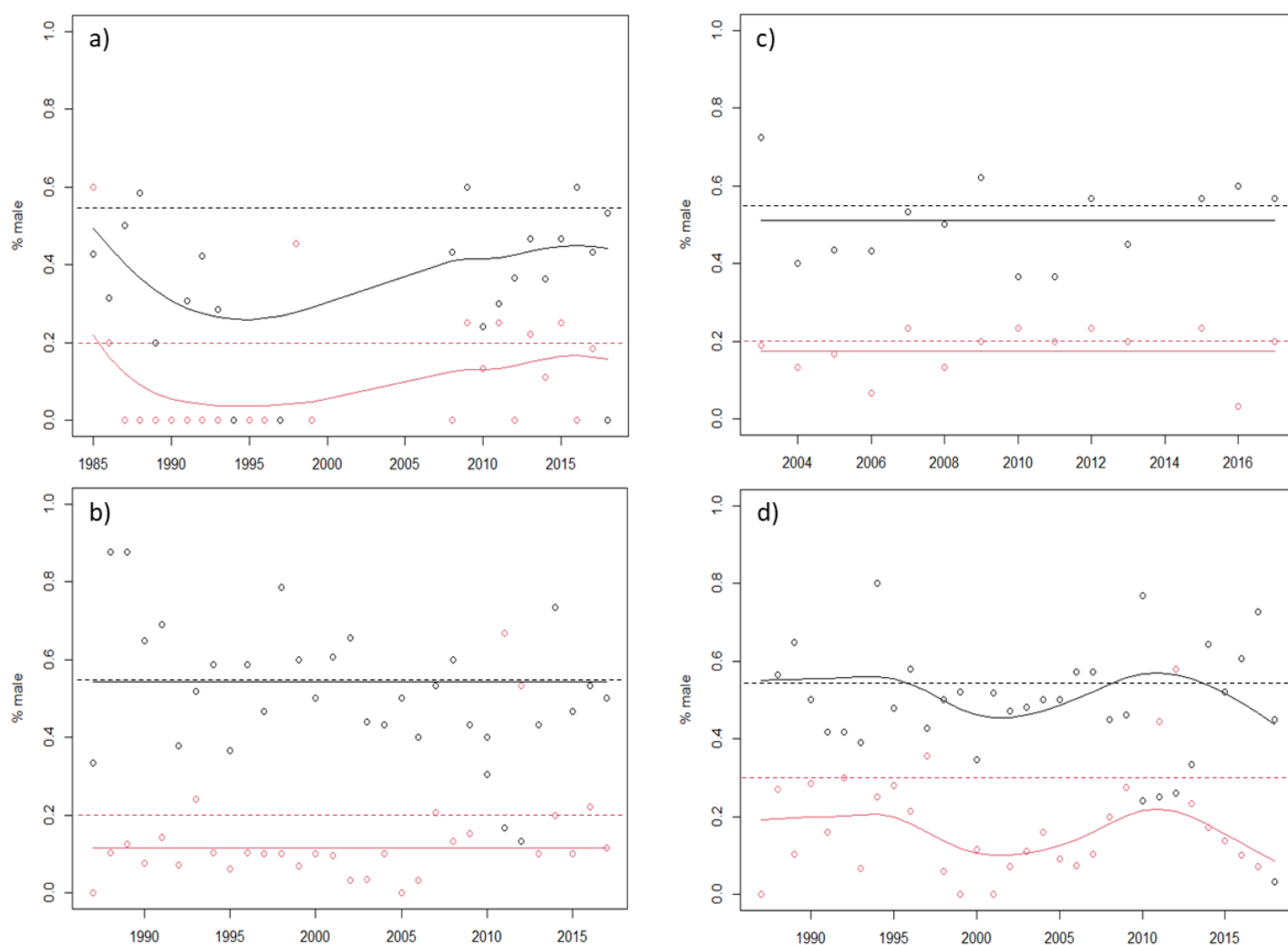
2. Changes in fecundity of salmonids

In salmonids, fecundity is driven strongly by female body length, and within a given age-class, the fecundity also depends on the sex-ratio. In SAMARCH, we provide individual level descriptions of phenotypes (body length, sex) to improve fecundity estimates at the population level, and to assess how fecundity might have changed over time in the context of recent changes in marine environmental conditions.

We developed a modelling approach that combines two steps: (i) based on individual data from females, we first model variations in fecundity as a function of body length; (ii) we model river-specific temporal trends in body length in our study populations; and then (iii) we combine the results of the two models to predict how temporal variation in body length might impact fecundity.

Modelling female fecundity as a function of body length

Data

We gathered 502 individual fecundity records collected in France to predict the number of eggs produced by female salmon as a function of their body length. Data was derived from Prévost et al. (1996), Dumas & Prouzet (2003) and ORE DiaPFC (Pers. com.). To limit sample size issues, the spatial resolution of the data was reduced to three bio-geographical regions, following Bal et al. (2017): Aquitaine, Bretagne, Normandie. The length-based fecundity model has not been updated for English populations due to unavailable fecundity data. Currently, the SAM for the England & Wales stock unit assumes the length-based fecundity relationship defined in Pope et al. (1961).

Statistical analysis

For any fish i originating from one of the 3 regions in France r (r=1, 2, 3), the effect of body length (L_{t_i}) on fecundity (Fec_i) was analysed using non-linear models of the form:
$$Fec_i = \alpha_r \times L_{t_i}^{\beta_r} \times e^{\epsilon_i}$$
where ϵ_i are identically and independently normally distributed random errors. In practice, models were fitted by regressing $\log(Fec_i)$ against $\log(L_{t_i})$ using the glm() procedure of R with a normal distribution and identity link function.

Results

As expected, we observe a positive relationship between fecundity and body length. In France, this relationship differs between regions, with females from Normandie producing a higher number of eggs for a given body length than females from Aquitaine and Bretagne (Figure 4). Compared to the relationship in French regions, the length-based fecundity model for England & Wales is characterised by a higher initial number of eggs for a 50 centimetre female and a shallower increase in fecundity for every extra

centimetre of body length. Nevertheless, it produces fecundity estimates that are generally comparable with estimates for France.

Figure 4. Estimated relationship between salmon female fecundity and body length in three French regions and England & Wales. Body length is defined as the total fish length.
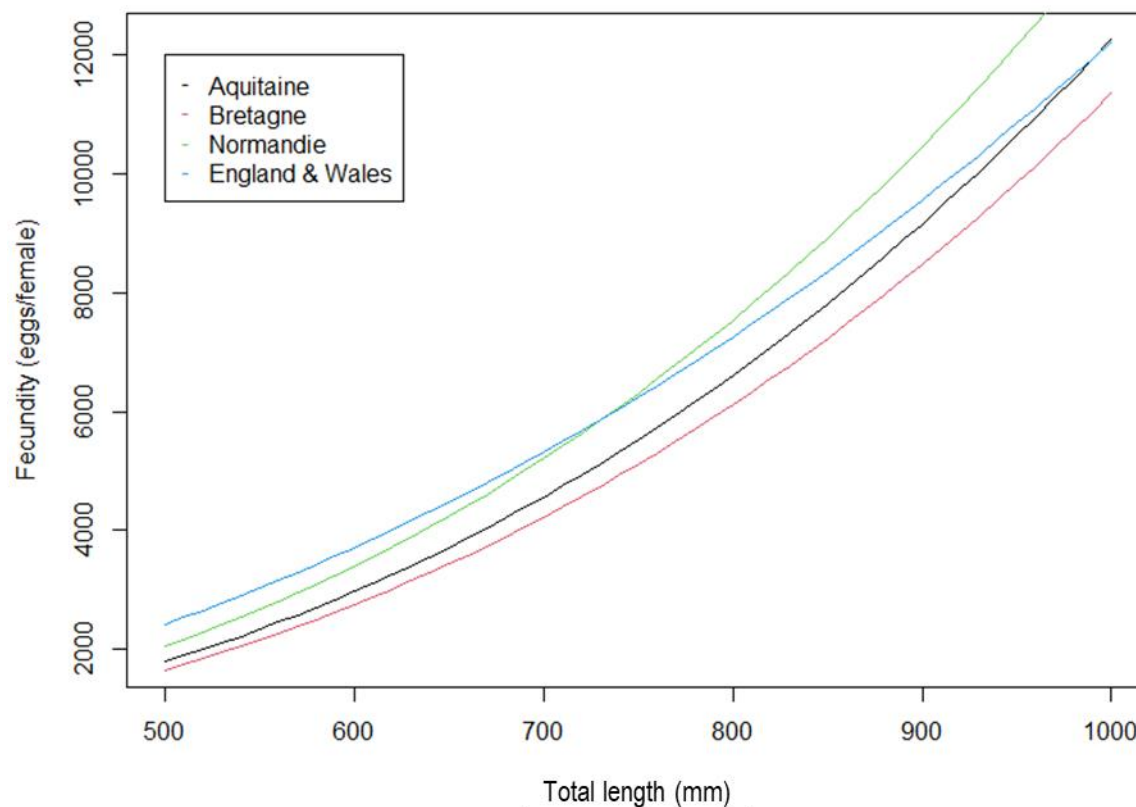
Modelling temporal change in body length

Data

We investigated temporal change in body length from a subsample of salmons caught at the traps and by anglers in the 5 SAMARCH rivers during their spawning migration (Table 2).

Rivers	1SW	2SW
Bresle	817	324
Sélune	887	919
Scorff	932	910
Frome	424	313
Tamar	514	488

Table 2. Number of individuals measured in the 5 SAMARCH rivers.

Body length, as used in the length-based fecundity model, refers to total fish length (L_t) and was estimated from fork length (L_f) measurements for salmon caught in the rivers Scorff (trap), Oir (trap), Tamar and Frome, following the relationship:

$$L_{t_i} = 2.804969 + 1.032038 \times L_{f_i}$$

Statistical analysis

Temporal trends in body length were analysed using generalized additive models (GAM; Wood, 2017) as implemented in the gam() function of the R-package mgcv, 1.8-31 (Wood 2017) to capture potential non-linearity in the trends. The effect of the sea-age class (1SW or 2SW) was introduced as categorical effect and the year was considered as a continuous variable in the non-parametric smooth trend. Independent models were built for smolts and adults for each river. The most complex model considered was:

$$Lt_i = A_i + s(Y_i, A_i) + \varepsilon_i$$

where Lt_i is the total body length for any fish i of sea-age A_i, caught at year Y_i , $s(Y_i, A_i)$ is a sea-age specific smooth time trend, and ε_i are independent and identically distributed residuals ~ N(0,σ^2). To test for the existence of trends specific to sea age, simpler nested models without time trend, or with identical time trend for each sea age were considered. Competing models were compared using AIC. No data transformation was needed as the residuals from the models did not reveal any departure from the assumptions of normality and homogeneity of variance.

Results

Results highlight a decrease in salmon body length over the study period in all SAMARCH rivers (Figure 5).

Figure 5. Change in body length over time in adult salmon returning to SAMARCH rivers: a) Bresle, b) Sélune, c) Scorff, d) Frome and e) Tamar. Annual mean (dots) and fitted temporal trends (lines) for 1SW (open dots and dashed lines) and 2SW (filled dots and solid lines) fish.
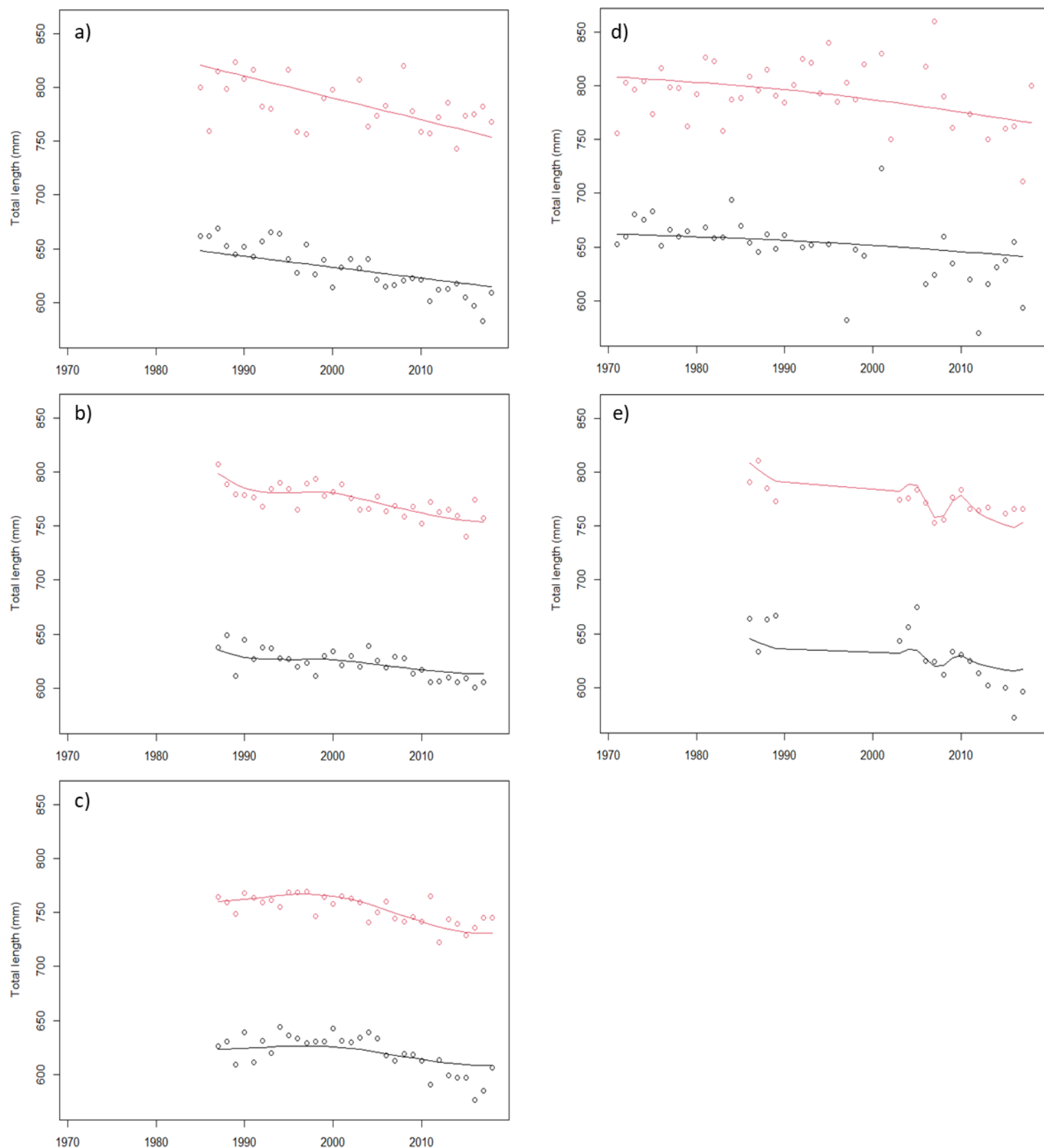
Estimating temporal change in female fecundity

### Coupling temporal trends in body length with length-fecundity-relationship

Models for temporal trends in body length in the different rivers were combined with length-fecundity models. Because the length-fecundity models are built at the scale of regions, temporal trends in fecundity were predicted by assigning the SAMARCH rivers to the Bretagne, Normandie or England & Wales regions. For each year and each river, the predicted length from the GAM model was used to predict the mean fecundity from the length-fecundity models.

Results

Results highlight a decline in female fecundity in both 1SW and 2SW fish that is shared by all the SAMARCH rivers (Figure 6). Because of the lower fecundity of females from Brittany compared to similar sized females from Normandy (Figure 4), female fecundity estimates in Scorff salmon appear even lower than the decline due to body length alone would suggest. Furthermore, our study illustrates that estimated fecundity for 2SW females in recent years falls below the fecundity value in stock assessment models currently used by ICES (France: 1550 eggs/1SW fish and 5520 eggs/2SW fish ; England and Wales : 1350 eggs/1SW fish and 4550 eggs/2SW fish). In contrast, ICES models systematically underestimate fecundity in 1SW.

Figure 6. Estimated change in female fecundity over time in adult salmon returning to SAMARCH rivers in 1SW (black dots) and 2SW (red dots) fish. Rivers: a) Bresle, b) Sélune, c) Scorff, d) Frome and e) Tamar. Following Figure 4, fecundity (Fec) was estimated from total length (Lt) and a regional effect (r) with Fec = exp(2.7730 *log(Lt)-r) and r = 9.8184 for Brittany and r = 9.6081 for Normandy. Fecundity for English populations was estimated from total length (Lt) with Fec = 10^(2.3345 *log10(Lt/10)-0.582)(Pope et al. 1961). The horizontal lines represent the value of fecundity of 1SW and 2SW females used in ICES stock assessment models for France (dashed line: line; ~~1550 eggs/1SW~~ fish and ~~5520 eggs/2SW~~ fish) and England and Wales (dotted line; ~~1350 eggs/1SW~~ fish and ~~4550 eggs/2SW~~ fish) stock units (ICES 2020).

France
1SW : 3500 œufs, MSW : 6900
UK and Wales
1SW : 3000, MSW : 5700
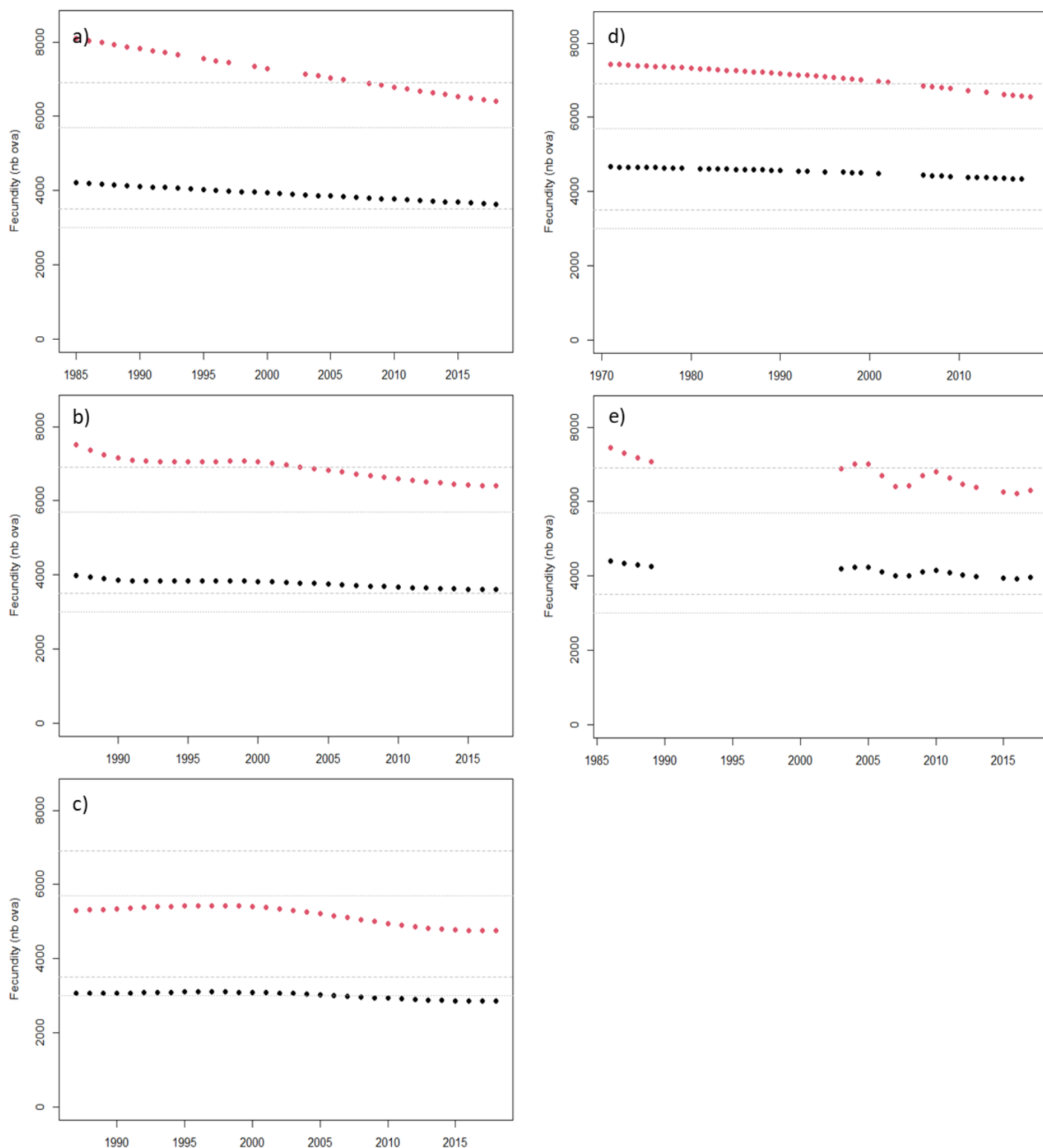
Estimating temporal change in egg deposition - Scorff as a case study

Egg deposition is typically computed as the product of the estimated number of returning adults per age class, the proportion of females per age class, and female fecundity per age class. Most stock assessment models assume a constant sex-ratio and fecundity in adults over time. However, by accounting for temporal trends in both sex ratio (Figure 2) and length-based fecundity (Figure 6), we can provide a more realistic estimate of egg deposition for a given stock or population.

Using the Scorff as a case study, we compare estimates of egg deposition as predicted with the values of sex-ratio and fecundity used by the ICES WGNAS model, and estimates of egg deposition as predicted with the updated values of sex-ratio and fecundity produced in SAMARCH (Figure 7). CL for the Scorff river is evaluate at 630000 eggs (ICES 2020).

Figure 7. Estimated change in egg deposition in the river Scorff using ICES WGNAS model (black line) and using SAMARCH updated sex-ratio and fecundity estimates (blue). The horizontal line represents the value of the conservation limit currently set up for the Scorff (CL = 630000 eggs ; ICES 2020).
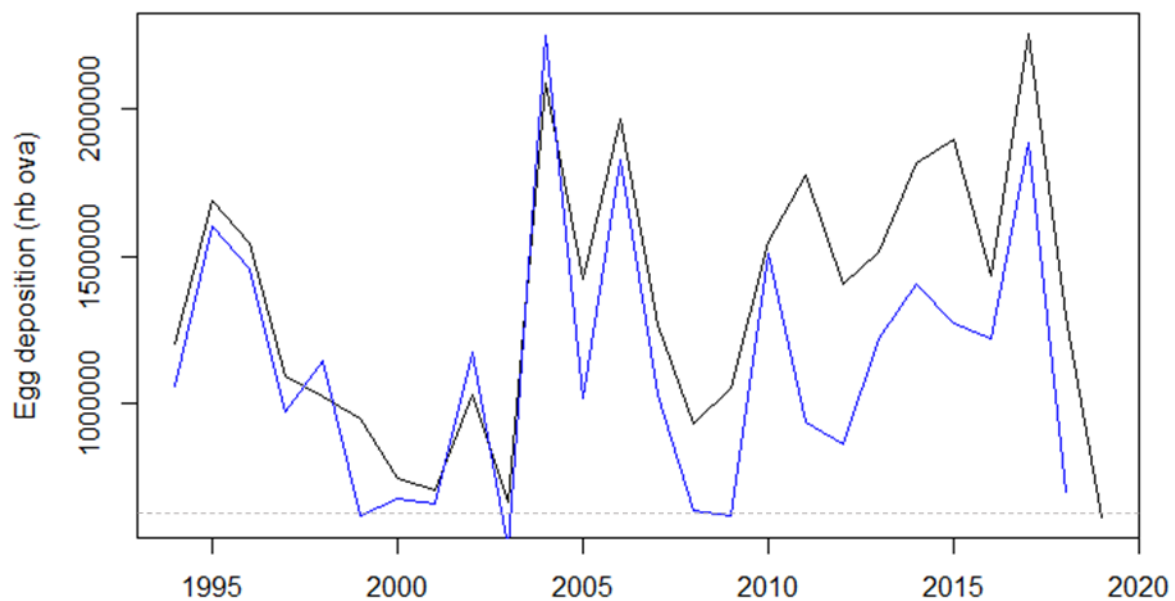
Discussion

Synthesis of the main results

In this report, we collate historical time series of biometric measures on fish sampled at traps and by anglers available for the 5 SAMARCH rivers. Individual measurements of length and fecundity available on a large sample of females were also collated. Those data were combined with new molecular sexing techniques developed in the SAMARCH project. All together, these new data and methods enable a timely assessment of long-term changes in the sex ratios at different stages of salmonids life cycle (smolts and adults) in the SAMARCH rivers. Statistical models where developed to characterize changes in sex ratios and female fecundity and investigate the factors that contribute to these changes (e.g. body size, age).

Results highlight that sex ratios of returning salmon were relatively stable for each sea age class over the study period. In contrast, the average fecundity of salmon declined by 15% between 1985 and 2018, driven mostly by a decline in the mean body length and weight of multi sea-winter females returning to the rivers to spawn. Using reference values from ICES, we illustrate that models routinely used to assess stock productivity and status may systematically overestimate egg deposition in recent years. As exemplified by salmon from the Scorff, this may lead to overestimation of compliance with conservation limits.

Perspectives

We focused our message on the average temporal trends in sex ratio, body length and mean fecundity in salmonids. However, our results rely on the assumption that the length-based fecundity relationship did not change over time, which may be questionable. In the face of a rapidly changing environment, there are growing evidence pointing at a rapid response of populations to evolutionary forces (Hairston et al. 2005, Carlson et al. 2011). In salmonids, widespread changes in the age structure of returning adults may suggest that such an evolutionary mechanism may be at play, which may compensate for, or exacerbate, the estimated decline in fecundity. In general, records of female fecundity are rare, scattered and generally old (from the 1970's and the 1980's), which prevent any detailed investigation of the temporal variability in length-based fecundity relationship. We call for greater attention to be paid in the future to the study of the fecundity of salmonids in the wild.

Careful assessment of uncertainties around temporal trends and their consequences on stock assessment are one of the most promising perspective of this study. In particular, following NASCO (NASCO 1998), compliance to conservation limits should be quantified as a risk (i.e. a probability) that the egg deposition falls below the CL (ICES 2020). Based on the Scorff example, we illustrate how considering new information about temporal trends in returning adults body size may impact point estimates of egg deposition. However, assessing how uncertainties propagates through the different modelling steps up to the estimates of egg deposition in index rivers is needed to accurately estimate

compliance to CL. Also, the estimate of CL itself is derived directly from stock-recruitment analysis, where the measure of "stock" is a point estimate of eggs deposited without considering its uncertainty (Prévost and Chaput 2001, Rivot et al. 2001). As our new results may lead to a revised time series of "stock" estimates, it would be pertinent to assess how new models may impact the estimate of the CL itself.

We recommend that our approach is generalized to other SAMARCH rivers and more widely to all index rivers in the North Atlantic basin considered by ICES. Given similar findings from other rivers around Southern Europe, for instance in Scotland (Bacon et al. 2009), trends in mean body size of returning adults appears to be a general pattern, and its consequence on estimates of egg deposition may be high (Glover et al. 2018).

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